

ECOLOGICAL-BEHAVIORAL STUDIES OF THE WASPS OF JACKSON HOLE, WYOMING

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ABSTRACT

During three summers of study, 190 species of wasps (Hymenoptera, Aculeata) were collected in Jackson Hole, Wyoming, principally in six selected sites along the Snake River. The majority of these were fossorial species, about 50 of which were found nesting. For the most part, the species studied appeared to avoid complete competition for prey and for nesting sites, but some possible exceptions are noted. Many species were attacked by parasitic flies, some by cuckoo wasps and other insects. Many of these natural enemies are not host-specific, and maintain high populations at the expense of many different species of wasps. The behavior patterns of the wasps are discussed as mechanisms for (1) avoiding competition with other wasp species, and (2) reducing the success of parasites. Following a general discussion of these subjects, a list of the wasps of Jackson Hole, annotated with ecological and behavioral data, is presented.

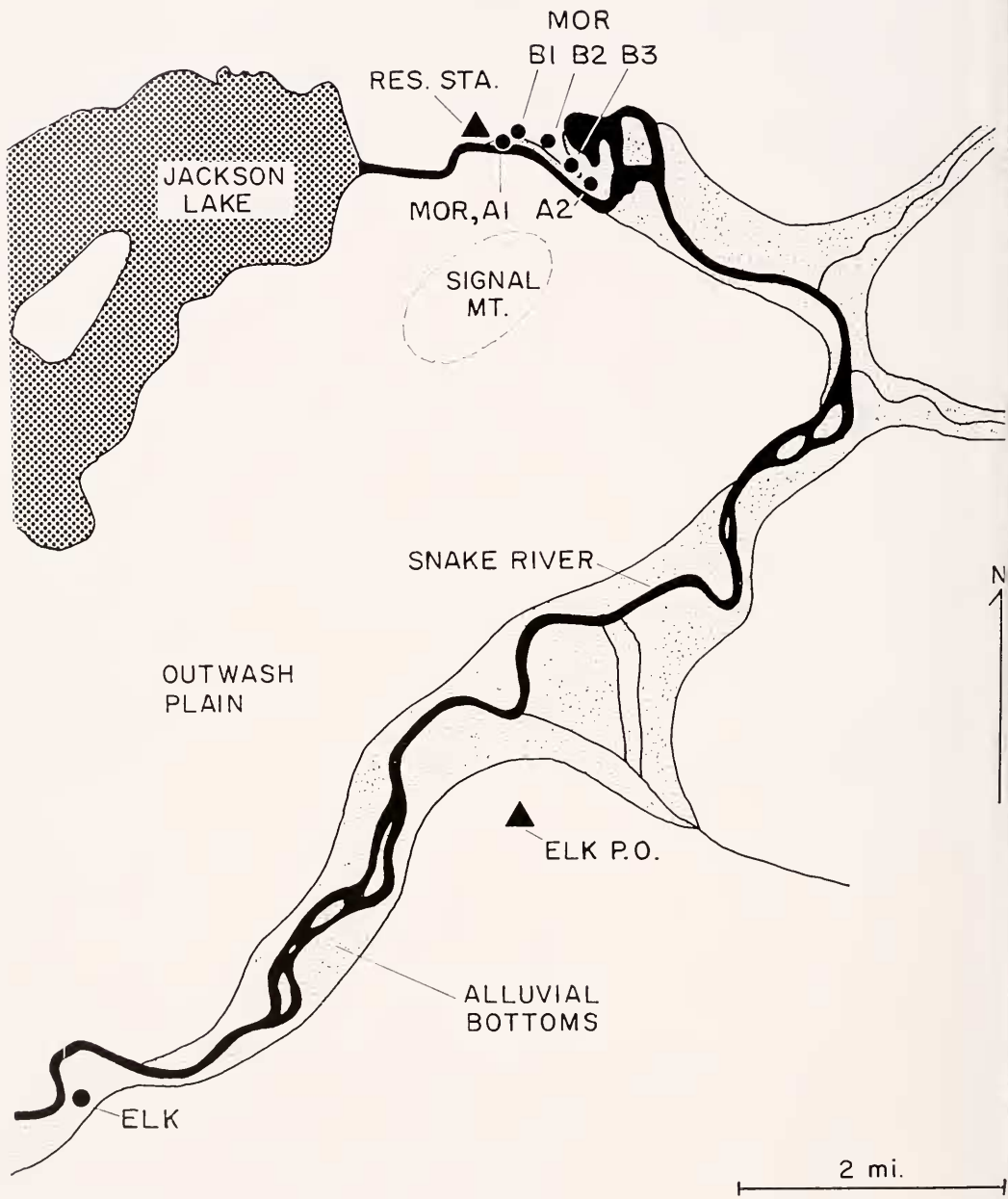
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INTRODUCTION

It was unfortunate that during the flowering of natural history in the 19th century it became fashionable to separate ecology (from *oikos*, home) from ethology (from *ethos*, habits). Surely the habitat and behavior of an animal are all of a piece. Behavior is merely the impingement of an animal upon its environment, while the environment is that portion of the biosphere in which an animal's behavior permits it to thrive. A biotic community is a collection of co-adapted behaviors, no one



Map 1. Sketch of portion of Jackson Hole, Wyoming, showing location of major study areas.

of which is fully understandable of and by itself. That such communities are often enormously complex is troublesome, but this should not divert us from assuming, at least occasionally, a broad view of the interactions of its components. Only such a view can provide insights into the adaptive value and biological significance of observed behaviors; and only behavioral studies can supply insights into the significance of the structures with which systematists are so preoccupied.

Most areas of bare, friable soil in temperate and tropical regions are inhabited by numerous species of digger wasps which often show marked behavioral differences with respect to nesting and hunting behavior. These behavior patterns are stereotyped and relatively easy to observe and to describe. Students have often concluded that the behavioral peculiarities of the various species represent adaptations for avoiding competition with other members of the community, or for reducing the incidence of attacks by the great numbers of parasites which occur in these restricted habitats. There have, however, been few efforts to consider an entire community in the attempt to document these impressions. The present study, although grossly incomplete, represents an effort in that direction.

Jackson Hole, Wyoming, is in many ways ideally suited for studies of this nature. This flat valley surrounded by mountains is relatively high (6750 feet elevation at Moran) and far enough north (about 44° north latitude) so that its insect fauna is more limited in species than that of many more southerly localities. Yet during the brief summer season insects are exceedingly abundant and much more diverse than one might expect, including species of eastern, Pacific coast, and northern distribution, as well as a few Upper Sonoran elements that apparently follow the Snake River drainage, and a few characteristic Rocky Mountain elements. From the point

of view of a specialist on digger wasps, the area is especially attractive because much of it is unsuitable for these insects; but those areas which are suitable (i.e., where the soil is friable and more or less devoid of vegetation) contain concentrations of species and individuals perhaps unrivalled anywhere. Another attractive feature is that much of Jackson Hole is part of Grand Teton National Park and thus immune to development or to extensive disturbance. Still another is the presence of the Jackson Hole Research Station at Moran, which provided a pleasant and effective base of operations during three summers of study (1961, 1964, and 1967). I am much indebted to the officers of the station, particularly to its director, Dr. L. Floyd Clarke, for facilitating this research in many ways. I am also indebted to the authorities of Grand Teton National Park for permission to collect specimens for identification.

STUDY AREAS

Most of the floor of Jackson Hole is classified as glacial outwash plain (Fryxell, 1930). East of Jackson Lake much loess has been deposited. This loess not only renders the glacial outwash relatively more friable than elsewhere, but also is the source of much of the alluvial sand which has been deposited here and there on the immediate banks of the Snake River. These studies were conducted partly in areas of "lower outwash plain" and partly in "alluvial bottoms," following Fryxell's terminology (see Map 1). The outwash plains are of Pleistocene origin (Wisconsin glacial stage) and consist chiefly of quartzite gravel with a variable content of loess and a great many cobbles of various sizes; for the most part they are covered with sagebrush (*Artemisia*). The alluvial sand is of recent origin; it is pale in color and of relatively uniform texture. It occurs in low terraces or in bars which often slope into the river, these bars and terraces often

being surrounded by willows and cottonwoods. Groves of lodgepole pine and aspen occur here and there in the outwash plain or adjacent to the alluvial deposits. Where the outwash gravels abut upon the river, the banks are usually high and are constantly being eroded, while the alluvial deposits are several feet lower and in areas of accretion during flooding. In some cases there is a bank separating the margin of the plain from the alluvial bottoms, but more often there is a gradual slope between the two with no sharply marked separation of soil type or cover.

Although I collected wasps at several places in Jackson Hole in an effort to understand the distribution of various species, most of my studies were conducted in three sites near the Research Station. These localities were chosen because of the high concentration of nesting wasps they contained and because each was slightly different as to soil type, vegetation, and composition of the fauna. The three sites are considered below, followed by a description of three additional areas in which extensive collecting was done. In each case I have noted the abbreviation by which these sites are indicated in the text. The three primary localities are shown on Map 1.

(1) Moran, area A (MOR-A). Alluvial sand close beside the Snake River, both near the Station (A1) and at the "Cattle Bridge," about 0.5 miles east of the Station (A2). These are areas of fine-grained, light sand, largely bare but in places partially overgrown with short grass or low herbs. The sand flats are relatively sharply separated from adjacent outwash plain and have a rich and distinctive fauna of digger wasps, including especially species of *Bembix*, *Oxybelus*, *Ammophila*, and *Tachysphex*. A2 is shown in more detail in Map 2, and a photograph of a portion of the area is shown in Figure 1.

(2) Moran, area B (MOR-B). Outwash plain between the Station and the Cattle Bridge, especially three areas with very

sparse vegetation (B1, 2, 3) which are inhabited by numerous species of wasps including *Philanthus pulcher*, *P. crabroniformis*, *Eucerceris* spp., and others (Fig. 2). Certain wasps occupied both the more friable portions of these areas and the more compact soil in the alluvial bars and terraces: such species as *Hoplisoides spilographus* and *Stenodynerus papagorum*. Wasps not largely restricted to either areas A or B are simply labeled "MOR" in the text. Since wasps nesting in A or B generally ranged widely for their prey, the two communities were by no means separate entities. Also, ground squirrels nesting in area B often produced mounds of loosened, friable soil which were occasionally occupied by typical inhabitants of alluvial sand such as *Episyrton quinquetatus*.

(3) Four miles SW of the Elk post office (ELK), roughly seven miles due south of MOR. This area is at a very slightly lower altitude (6650 feet) and is one in which the rather extensive alluvial sand grades almost imperceptibly into glacial outwash, the two soil types intergrading over a low terrace of several acres (Fig. 3). The rich wasp fauna here is dominated by *Bembix americana spinolae* and *Philanthus zebratus nitens*.

(4) Five miles north of the city of Jackson, near the junction of the Gros Ventre and Snake Rivers (JAC). This is at a still lower altitude (6300 feet) and represents an area of extensive alluvial deposits of cobblestones with patches of sand.

(5) Pilgrim Creek (PCR), in Grand Teton National Park and Teton National Forest, some four to seven miles NE of Moran. This is a small stream cutting through forested country, but having numerous sandy deposits along its banks. The sand-inhabiting wasps are similar to those in MOR-A; in addition, there are many twig-nesting wasps here, as is generally true in more wooded areas.

(6) Huckleberry Hot Springs (HHS), in Teton National Forest just north of Grand

Teton National Park and south of Yellowstone. This area is of special interest because of its hot springs, which favor certain species of generally more southerly distribution (e.g., *Bembix amoena*). Studies were conducted in a sandy field adjacent to the major springs.

MAJOR ASPECTS OF ECOLOGY

During the period of study, 190 species of aculeate wasps were collected in these six areas (six other species, listed below in brackets, in peripheral localities). Some species were taken only once or twice and appear to maintain low populations in Jackson Hole, while others were exceedingly abundant in suitable sites. The majority of these wasps (slightly over 100 species) are solitary ground-nesters or are parasites of such wasps. How do so many species of generally similar behavior manage to survive side-by-side during the same brief active season, especially when the presence of so many fossorial wasps permits the build-up of great numbers of parasites? To what extent are the observed behavioral differences among these species understandable in the contexts of interspecies competition and of rampant parasitization? An attempt will be made to answer these questions in this and the next section, leaving the actual documentation to an annotated list of wasps to follow.

I was able to study the nesting and predatory behavior of only about half of the ground-nesters (about 50 species in all), but these were by and large the commoner fossorial species. The majority of the other species have either been studied elsewhere or are closely related to species of known behavior. While most of the conclusions I shall draw here are based on those species studied in detail in Jackson Hole, there is basis for extrapolating them to the remainder of the wasp fauna.

SEASONAL CYCLES

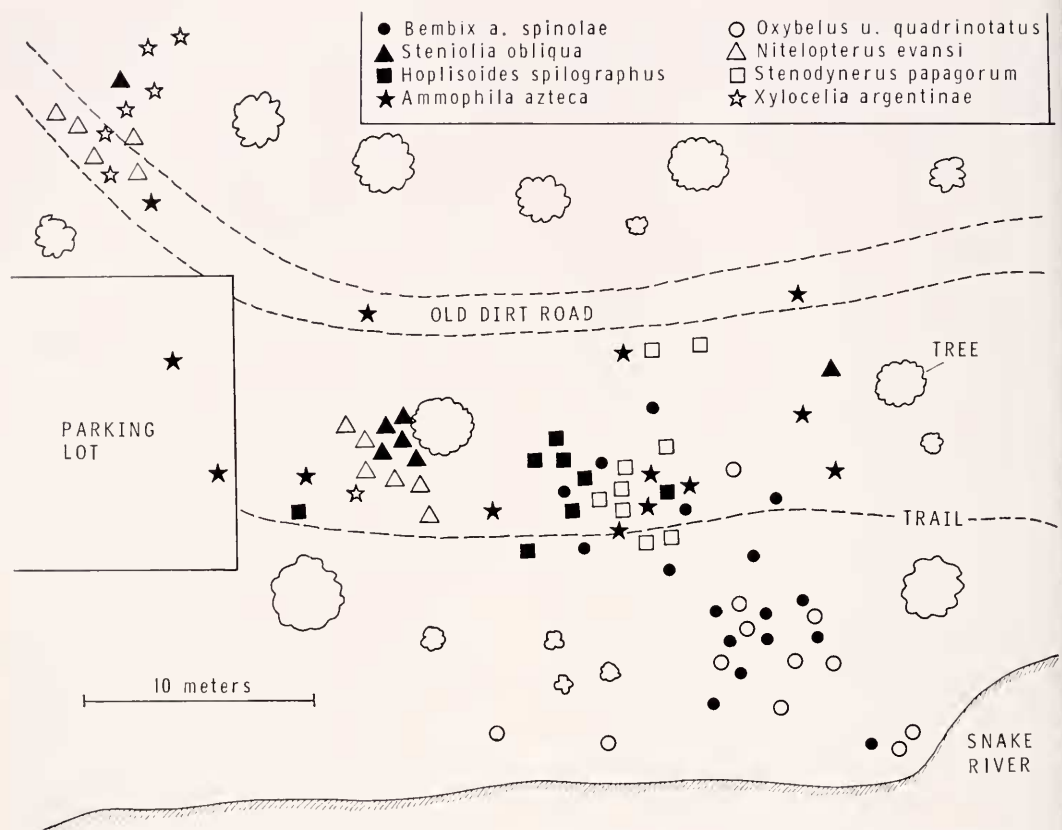
Since adult female solitary wasps generally live from three to six weeks, it is

obvious that to thrive in Jackson Hole they must emerge some time in July in order to have time to complete their nesting cycles before cold temperatures restrict activity in late August or early September. Hence, most species nest more or less simultaneously. Nevertheless some differences in time of emergence and completion of nesting can be noted. For example, *Philanthus pulcher* emerges in late June or early July and has largely disappeared by August first, while *P. pacificus* is a species characteristic of August. Among the spider wasps, *Episyrion quinquevittatus* is already active in early July, while *Ageniella blaisdelli* does not appear until about August 1. However, differences in seasonal cycle apparently functioning to reduce competition among species are minimal in this area.

NESTING SITES AND NEST TYPE

Most of the fossorial wasps studied nested in one particular type of soil and no other. *Bembix americana spinolae*, for example, is a gregarious species requiring a fairly large expanse of fine-grained, friable sand; populations of this species occurred only at MOR-A2, ELK, and HHS. The related wasp *Steniolia obliqua*, in contrast, occurs in smaller aggregations in patches of coarser soil, not necessarily entirely bare (although this species is highly gregarious at night and during unfavorable weather, forming massive "sleeping clusters" on vegetation). This species nested at MOR-B3 and on the periphery of A2, in no case forming mixed nesting aggregations with *Bembix*. The differences among the five species of *Philanthus* with respect to soil type are summarized in a subsequent section.

While related wasps in many cases tend to occupy slightly different soil types, any one site often contains a diversity of species belonging to different genera (a widespread phenomenon studied by Elton, 1946). If the soil is of uniform texture, the nests of different wasps may be interspersed, but more often there is some



Map 2. Detailed map of study area MOR-A2, showing location of marked nests of 8 species over a period of several days in late July, 1964. There were many more, unmarked nests of each of these species as well as nests of numerous other species.

tendency for segregation of species in accordance with minor differences in consistency of the soil. Location of nests of some of the species occurring in MOR-A2 are shown in Map 2 (see also Fig. 1). In this community, certain wasps (notably *Bembix* and *Oxybelus*) tended to occupy the very friable sand near the river, certain others occupied more compact sand along trails and roads (especially *Ammophila* and *Stenodynerus*), while still others occupied places in partial shade or with more ground cover (*Steniolia*, *Diodontus*). In this site, the eight species listed on the map all nested in great numbers during late July and early August, along with many other species, some of them nearly

or quite as abundant as those listed (e.g., *Episyron quinquenotatus*, *Nitelopterus evansi*, *Podalonia communis*). Thus the scene in midsummer is one of constant activity involving many hundreds of ground-nesting wasps belonging to literally dozens of species.

Moving to a neighboring site of quite different soil type (e.g., to MOR-B3; Fig. 2), one finds a rather different set of wasps, in this case dominated by species of *Philanthus*, *Pisonopsis*, and *Belomicrus*, but with several species in common with A2: *Astata nubecula* and *Steniolia obliqua*, for example. Each of the areas studied had its own particular complex of species, with some overlap in content with other areas;

yet much the same parasites (particularly miltogrammine flies) occurred in all areas in considerable numbers.

Even bare places only a few square meters in extent (such as MOR-B2 and B3) are able to support many fossorial wasps. The nest burrows and entrances are, after all, only a few millimeters in diameter, and each nest is a temporary affair, being permanently closed and abandoned after the completion of provisioning (this is less true of Philanthinae, many of which maintain a single, multicellular nest for their entire lives). Female wasps of the same or different species nesting in close proximity rarely show extensive aggression toward one another; thus, it is possible for many nest-cells to be packed into a limited space. To a certain extent the cells tend to be stratified, for some species make very shallow nests, others relatively deep ones. Nest depth is not necessarily correlated with size of the wasp, for some large species (for example, all species of *Ammophila*) make their nest-cells only a few centimeters beneath the surface. Stratification of nest-cells is well shown in the sandier parts of MOR-A2, where excavations during the inactive season reveal many cocoons of *Bembix americana spinolae* at a depth of about 8 cm (range 5–11 cm) and many of the smaller cocoons of *Oxybelus uniglumis quadrinotatus* at a depth of about 5 cm (range 3–7 cm). An assortment of typical nests from MOR-A2, drawn to the same scale, is shown in Plate V.

While most attention was focused on fossorial species in this study, it should be pointed out that many of the 190 species recorded from Jackson Hole do not nest in the soil but above ground in trees, bushes, or herbs. Some of them nest in hollow twigs (e.g., Eumenidae such as *Ancistrocerus* and *Symmorphus*), others bore in pith or rotten wood (e.g., Sphecidae such as *Ectemnius* and *Pemphredon*), still others build mud nests on stems

(*Eumenes*), or on rocks (*Pseudomasaris*), or paper nests in trees, shrubs, or cavities in the soil (Vespididae). It is usually considered that the primitive wasps were fossorial and that various groups have transferred to aerial nesting sites, thus freeing themselves from an attachment to bare, friable soil and from competition with soil-nesters. Competition for hollow twigs is, however, often severe (though not studied here). In the areas of study, twig-nesters were especially prevalent at PCR, which is heavily wooded. Since nesters in the restricted areas of bare soil in Jackson Hole did most of their foraging for prey in surrounding vegetation, and since ground-nesters and aerial-nesters often fed on the nectar of certain flowers side by side, it cannot be said that ground-nesters and aerial-nesters occupied fundamentally different food sites. From the point of view of adult and larval food, they were members of one community, and from the point of view of nesting sites, of two. It should be added that the parasites of aerial-nesters are almost totally different from those of ground-nesters; evidently very different behavioral adaptations are required for exploiting nests in the two situations.

FOOD RELATIONSHIPS

Collectively, the wasps of Jackson Hole prey upon virtually all kinds of arthropods available in quantities. Yet to a remarkable degree they "divide up" the prey, each species of wasp specializing on one or a few kinds. A general summary of the prey of the commoner fossorial species is presented in List 1, where the wasps are arranged systematically. Consideration of the prey systematically is also instructive. For example, spiders are exploited as prey by at least two species of Sphecidae and by numerous Pompilidae. Yet any one family of spiders is often utilized by only one predator:

Dictynids (Dictynidae) by *Nitelopterus evansi*

Combfooted spiders (Theridiidae) by *Pisonopsis clypeata*
 Orbweavers (Araneidae) by *Episyron quinquenotatus*
 Crab spiders (Thomisidae) by *Dipogon sayi*
 Jumping spiders (Salticidae) by *Pompilus angularis*
 Wolf spiders (Lycosidae)
 Large *Lycosa* by *Pompilus scelestus*
 Medium-sized *Lycosa* by *Cryptocheilus terminatum*
 Small lycosids by *Pompilus occidentalis*, *Anoplius tenebrosus*.

LIST 1

Prey of commoner ground-nesting wasps of Jackson Hole (wasps arranged systematically; see Annotated List, beginning p. 474, for details)

TIPHIIDAE: 3 spp. – Beetle larvae in soil (Coleoptera)

EUMENIDAE

Stenodynerus papagorum – Leaf-mining beetle larvae (Coleoptera)

POMPILIDAE

Cryptocheilus t. terminatum – *Lycosa* spiders (immature) (Araneae)

Episyron q. quinquenotatus – *Araneus* spiders (Araneae)

Pompilus angularis – Small errant spiders, mostly Salticidae (Araneae)

Pompilus scelestus – *Lycosa* spiders (adult) (Araneae)

SPHECIDAE

SPHECINAE

Palmodes carbo – *Cyphoderris* (Gryllacrididae) (Orthoptera)

Palmodes hesperus – *Anabrus* (Tettigoniidae) (Orthoptera)

Podalonia communis – Soil-inhabiting larvae of Noctuidae (Lepidoptera)

Ammophila azteca – Larvae of small moths or of sawflies (Lepidoptera, Hymenoptera)

Ammophila dysmica – Larvae of leaf-feeding Noctuidae (Lepidoptera)

Ammophila macra – Larvae of Sphingidae (Lepidoptera)

PEMPHREDONINAE

Diodontus: 3 spp. – Aphids (Hemiptera)

ASTATINAE

Astata nubecula – Pentatomidae, immature (Hemiptera)

Dryudella montana – Reduviidae, Scutelleridae, Cydnidae (Hemiptera)

LARRINAE

Plenoculus d. davisii – Miridae, adult and immature (Hemiptera)

Solierella affinis – Nabidae, immature (Hemiptera)

Niteloater evansi – *Dictyna* spiders (Araneae)

Pisonopsis clypeata – Theridiid spiders (Araneae)

Tachysphex: 5 spp. – Acridid grasshoppers, immature (Orthoptera)

CRABRONINAE

Lindenus columbianus – Small parasitic wasps, flies, and bugs (Hymenoptera, Diptera, Hemiptera)

Crossocerus maculiclypeus – Very small flies (Diptera)

Belomicrus f. forbesii – Miridae (Hemiptera)

Oxybelus uniglumis quadrinotatus – Diverse small flies (Diptera)

NYSSONINAE

Gorytes canaliculatus asperatus – *Idiocerus* leafhoppers (Hemiptera)

Hoplisoides spilographus – Immature treehoppers, Membracidae (Hemiptera)

Stictiella emarginata – Adult moths, Noctuidae (Lepidoptera)

Steniolia obliqua – Beeflies, Bombyliidae (Diptera)

Bembix americana spinolae – Diverse, medium-sized flies (Diptera)

PHILANTHINAE

Aphilanthops subfrigidus – Queen *Formica* ants (Hymenoptera)

Philanthus: 5 spp. – Bees and wasps (Hymenoptera)

Eucerceris flavocincta – Adult, medium-sized weevils (Coleoptera)

Eucerceris fulvipes – Adult, very small weevils (Coleoptera)

In some cases this specialization in predation is absolute; for example, there are now literally hundreds of records from many areas which indicate that *Episyron quinquenotatus* takes only orbweavers. In other cases there is overlap which is more apparent than real: *Pisonopsis chlypeata*, for example, takes an occasional orbweaver, but only small species occurring close to the ground and not utilized by *Episyron*. Inclusion of other, less common Pompilidae in this listing would complicate the picture, but by no means smudge it completely. Two species of *Aporinellus*, for example, prey upon Salticidae, but these are very small wasps and undoubtedly take smaller spiders than *Pompilus angularis*. A number of small Pompilidae besides those listed are known to employ small lycosids, e.g., *Anoplius ithaca*, *A. imbellis*, *Priocnemis notha*, and some of these use errant spiders of other families as well. It is probable that *Cryptocheilus* utilizes immature *Lycosas* which, when mature, might serve as prey for *Pompilus scelestus*. Thus, there would appear to be competition for prey among the numerous predators on errant spiders. Two points should be made here: (1) these are abundant spiders, readily available and not requiring highly specialized hunting behavior; and (2) the wasps involved are parasitized by certain Pompilidae (*Ceropaes*, *Evagetes*) and by miltoigrammine flies, and their populations may thus be suboptimal. I would assume that most pompilids, like many other insects, occur at relatively low densities as a result of parasite pressure and thus are able to occupy similar or even identical food niches. In any case, the pompilids in question have different nesting behaviors and often occupy different nesting sites;

thus, they are by no means ecological homologues. For example, of the two predators on small lycosids listed, *Pompilus occidentalis* nests primarily in wooded areas, *Anoplius tenebrosus* in open country.

Examination of the predators on major groups of insects reveals situations similar to that prevailing among the spider-hunters. The fauna of Jackson Hole includes quite a number of predators on Orthoptera. Two species of *Palmodes* take large long-horned grasshoppers; present records indicate that they use different species, but this may not hold up. *Larropsis capax* is known to utilize camel crickets (*Ceuthophilus*). Five species of *Tachysphex* use immature short-horned grasshoppers (Acrididae), but these species are not all the same size. Furthermore, the larger species use one grasshopper per cell, hence, they take grasshoppers slightly larger than themselves, while the smaller species use several per cell and generally use grasshoppers smaller than themselves. Hence, the spread in size of prey is greater than that in size of the wasp. The following is a list of the species of *Tachysphex*, giving the mean length of the females and the mean length of the grasshoppers utilized (in the case of *aethiops* and *nigrior* only one prey each was taken; see Annotated List for data).

Species of <i>Tachysphex</i>	Mean length of females	Mean length of prey
<i>aethiops</i>	13.0 mm	16.0 mm
<i>tarsatus</i>	9.5 mm	10.0 mm
<i>nigrior</i>	9.0 mm	9.5 mm
<i>terminatus</i>	7.5 mm	6.5 mm
sp. nr. <i>linsleyi</i>	6.5 mm	6.0 mm

Since these species nest more or less simultaneously, and since each species of grasshopper tends to be at one growth stage at this season, it is unlikely that the species of *Tachysphex* at the ends of this spectrum often use the same species of prey. However, by presenting only the means I have concealed the fact that each species takes grasshoppers over a considerable size range (see especially Kurczewski, 1966). Undoubtedly considerable overlap

in prey does occur, and much the same reasoning may apply as in the case of the spider-hunters.

The predators on Coleoptera seem to show little overlap in prey preferences. *Eucerceris flavocincta* is a large wasp using rather large weevils, *E. fulvipes* a smaller wasp using very small weevils. Leaf-mining larvae of weevils and leaf beetles are employed by *Stenodynerus papagorum*, and it is probable that here as elsewhere twig-nesters of the genera *Symmorphus* and *Leptochilus* utilize beetle larvae feeding externally on leaves. The species of *Tiphia* presumably attack the subterranean larvae of scarab beetles here as elsewhere, and *Methocha* the larvae of tiger beetles.

Quite a number of wasps in Jackson Hole employ Lepidoptera as prey. Of the two that are known to employ adult moths (though not actually studied here), *Stictiella emarginata* uses Noctuidae, the twig-nester *Lestica interrupta* small Microlepidoptera. Species employing lepidopterous larvae include especially several *Podalonia* (using subterranean larvae or "cutworms") and several *Ammophila* (using external leaf feeders). Among the *Ammophila*, *macra* uses very large sphingid larvae, *dysmica* medium-sized Noctuidae, *azteca* small larvae of Geometridae and other groups, including sawflies, and *pilosa* uses principally larvae of lycaenid butterflies. Five other less common species of *Ammophila*, unstudied in this area, may well show some prey overlap with these species. Many aerial nesters also utilize lepidopterous larvae, *Ancistrocerus catskill*, for example, is common in Jackson Hole; this species uses small Microlepidoptera and thus may not compete seriously with any of the ground-nesters. Some of the other Eumenidae may, however, do so.

In the case of the several predators on Diptera nesting in the ground, some slight overlap in prey is apparent between *Steniolia obliqua* and *Bembix americana spinolae* and between the latter species and

Oxybelus uniglumis quadrinotatus; *Crossocerus maculiclypeus* utilizes extremely small flies not otherwise employed by any ground-nesters studied. There are major gaps in knowledge here, as species of *Crabro* (ground-nesters) and *Ectemnius* (nesters in wood) were common in Jackson Hole and are predators on Diptera: however, I obtained no prey records and thus cannot compare them directly with the species studied.

In the case of predators on true bugs (Hemiptera), it should be pointed out that *Astata nubecula* preys on fairly large stinkbugs, *Dryudella montana* on small, immature bugs of several related families, *Plenoculus davisii* and *Belomicrus forbesi* on plant bugs (Miridae) (but so far as known on different species). Other Hemiptera-predators attack treehoppers (*Hoplisoides*), leafhoppers (*Gorytes* and presumably *Dienoplus*, *Mimesa*, *Crossocerus wickhamii*, and the Dryinidae), and aphids (various Pemphredoninae, including three species of *Diodontus*). Leafhoppers and aphids are exceedingly abundant insects, and it is not surprising that they are attacked by a variety of wasps. None were studied in sufficient detail to determine how much prey overlap occurred, but it can confidently be said that the wasps involved are diverse in habitat and nest type. For example, two of the three species of *Diodontus* were common, yet one was confined to friable, flat sand at MOR-A2, the other to roadside banks of coarse glacial outwash at MOR-B3.

Rather than prolong this discussion, I should like to consider one other group in greater detail: the species of *Philanthus*, predators on wasps and bees, and among the most abundant wasps in Jackson Hole. These exhibit ecological displacement in an unusually striking manner and also serve to point up the great complexity of communities such as this, for several species utilize as prey fossorial wasps nesting close to them, while some utilize the parasites of wasps or of their prey.

ECOLOGICAL DISPLACEMENT IN THE SPECIES OF *PHILANTHUS*¹

Despite the abundance of members of this genus in Jackson Hole, it is an unusual experience to encounter more than one species at one time and place. At MOR-B, *P. pulcher* is a dominant species through July, each female making a series of rather shallow nests (Fig. 36) in bare places relatively free of stones; during three summers, I have never collected or seen this species after August 3. *P. crabroniformis* is an equally abundant species, making its first appearance about July 22, but beginning to nest in numbers a week or so later. On a few occasions I have seen *crabroniformis* females digging in sites occupied by *pulcher*, but for the most part they select places where the soil is notably harder and stonier. Since wasps of this species make relatively deep, complex nests which they usually occupy for life, and since all expansion of the nest is at lower soil strata (Fig. 38), friability of the surface soil is evidently less critical. Mean cell depth of *pulcher* is 8.3 cm (range 6–10 cm), while that of *crabroniformis* is 13 cm (range 9–21 cm). *P. pulcher* preys upon bees and wasps in approximately equal numbers, including such diverse forms as cuckoo wasps, leaf-cutter bees, and several parasitic bees (List 6). Most of these are small insects, but a few are about as large as *P. pulcher*; the mean length of females of this species is 10 mm, the mean length of the prey 6 mm (range 4–11 mm).²

P. crabroniformis, on the other hand, although averaging slightly larger than *pulcher*, uses a great many halictid bees much smaller than itself; only occasionally does this species employ wasps as prey (List 7). The mean length of female *crabroniformis* is 11.5 mm, that of the prey only 5.5 mm (range 4–8 mm). One species of wasp and six species of bees appear on both lists of prey; 15 per cent of the species utilized by *pulcher* were also utilized by *crabroniformis*, but these make up about one third of the records for *pulcher* (species of *Dialictus* being the most commonly used prey of both species). Thus there is a fair amount of overlap in prey, the larger species curiously tending toward smaller prey than the smaller. However, the two species displace one another almost completely with respect to soil type and stratum and with respect to nesting season. In the final analysis, they may be characterized as non-competitors.

A third species, *P. pacificus*, appears in late July, at about the same time as *crabroniformis*. It is a considerably smaller species (mean length of females about 9 mm), yet a comparison of available prey records reveals that the two compete for much the same bees and wasps (mean length of prey of *pacificus*: 5.2 mm, range 4–7 mm). Both use only an occasional small wasp, but use ground-nesting bees in great numbers, small Halictidae making up 78 per cent of the prey of *pacificus*, and 96 per cent of the prey of *crabroniformis*. The majority of species taken as prey by *pacificus* (List 9) also appear on the list for *crabroniformis*. Evidently these bees are sufficiently abundant in August to support aggregations of two species of *Philanthus*. However, these two wasps exhibit a total separation in nesting sites, *pacificus* being confined to fine-grained,

¹ I use the word "displacement" to refer to different ways of exploiting the habitat, not in the sense of physical displacement of one species by another. That is, a species occurring in a particular area and habitat will have features which are displaced by other features in related species also occurring there. Darwin (1859) spoke of this as "divergence of character" and stressed that "more living beings can be supported in the same area the more they diverge in structure, habits, and constitution" (Mayr, 1963).

² Length of the prey is a poor measurement of size, since bees and some wasps are notably

broader and heavier than such wasps as *Mimosa*, *Ammophila*, etc. However, it was the only convenient measurement I could make with the available time and facilities.

light sand in bars close beside the river (at MOR-A2) or in the center of sandy roads near the river (at ELK). In no case did I find these two species nesting within 200 meters of one another. Like most *Philanthus*, they probably do most of their hunting on flowers (taking many more male bees than females), and it is probable that they exploit different patches of *Solidago* and other flowers, at least for the most part.

A fourth species of *Philanthus*, *zebratus nitens* (referred to hereafter simply as *zebratus*), appears in mid-July and is active until mid-August. This is a large, colorful species which nested in large numbers in moderately friable sandy soil at ELK and also along a sandy road at HHS; I did not take the species at MOR at any time. At ELK, *zebratus* occupied more hard-packed sand than *pacificus*, and at HHS more friable sand than *crabroniformis*. I would characterize this species as preferring a soil type intermediate between those two species, and the absence of a suitable expanse of such soil at MOR may explain its absence there. In any case, *zebratus* exhibits almost no prey overlap with either of those species, since it uses notably larger prey. The mean length of female *zebratus* is about 14 mm, the mean length of the recorded prey 11.3 mm (range 8–18 mm). This figure is somewhat deceptive, since the longer prey consisted of Ichneumonidae and such Sphecidae as *Ammophila*, which are very slender-bodied. Nevertheless, *zebratus* does clearly occupy a different food-size niche than *pacificus* and *crabroniformis*; no species and only one genus appear in common on the lists for *pacificus* and *zebratus* (List 8), and only one species and two genera in common on the lists for *crabroniformis* and *zebratus*. As a predator, *zebratus* has much more in common with *pulcher*, since it uses wasps and bees in about equal numbers and uses prey averaging only slightly smaller than itself. The prey lists for these two species have five

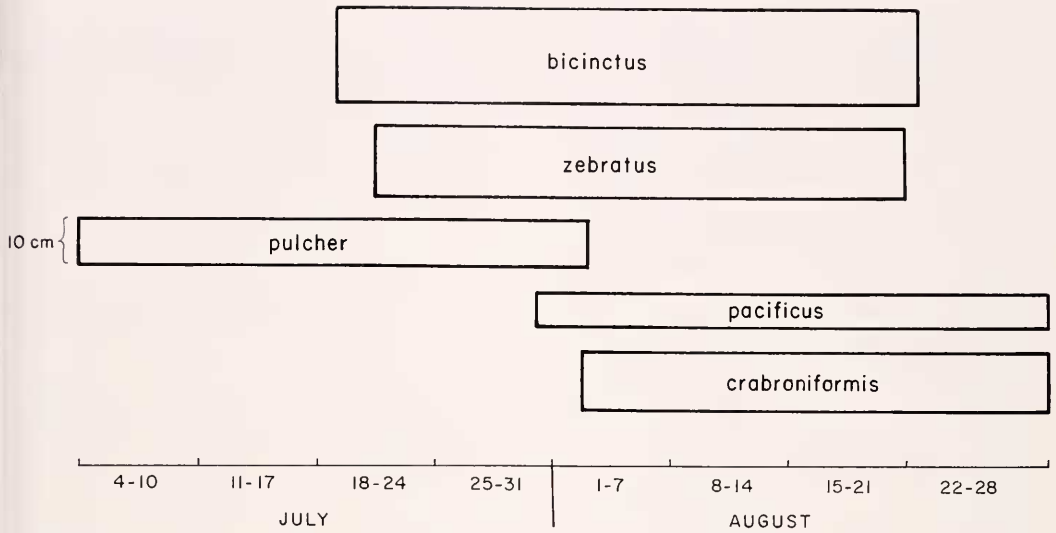
genera (no spp.) of wasps and eight genera (3 spp.) of bees in common. However, I found the two species nesting in the same situation only once (at ELK) and then on a date (July 10) when only *pulcher* was nesting.

The fifth species of *Philanthus* occurring in Jackson Hole, *bicinctus*, I shall discuss only briefly, since I encountered it only occasionally, and since Armitage (1965) has discussed a nesting aggregation at the South Gate of Yellowstone. This species makes very deep nests in thinly vegetated slopes where the soil is very coarse and stony; the prey consists principally of bumblebees of several species, rarely of other large bees. Thus it is isolated from the other four species both with respect to habitat and with respect to prey.

Differences among the five species in seasonal cycle and size of the females are summarized in Text-figure 1; however, it should be remembered that size of the wasp is not a wholly dependable reflection of size of the prey, for *crabroniformis* uses prey averaging smaller than *pulcher*. Also, the figure makes no attempt to indicate differences in soil type utilized for nesting, which (although characterized here only subjectively) is evidently at least slightly different in each of the five species, and quite conspicuously different in some cases (e.g., *pacificus* vs. *crabroniformis*). Some of the several conspicuous behavioral differences between the five species evidently serve to sustain the almost complete ecological displacement among these species. Others probably serve to maintain reasonably high population sizes in spite of the presence of an abundance of parasites. It will be more profitable to explore this subject after surveying the parasites briefly.

KINDS AND SPECIFICITY OF PARASITES AND PREDATORS

The approximately 100 species of ground-nesting wasps occurring in the areas of study were attacked by a consider-



Text-figure 1. Comparison of the five species of *Philanthus* occurring in Jackson Hole with respect to mean size of females (width of bars) and period during which females provision their nests.

able array of parasites and predators¹; 25 species of Diptera and Hymenoptera were either actually shown to attack these wasps, or can be assumed to attack them with a high degree of probability. Some of these are relatively host-specific, attacking one or a few related species of wasps, while others show little or no specificity, attacking ground-nesters of many diverse species. Specificity implies a measure of coevolution of host and parasite; that is, the two may acquire behavioral traits that permit them to coexist without marked population depressions. On the other hand, non-specific parasites may have varying success depend-

ing upon the behavior of their host, which cannot usually have evolved behavior patterns fitted to reducing the success of all of its various attackers. Thus, non-host-specific parasites and predators may be more significant in producing population crashes in certain hosts ill-adapted to them and in bringing about rapid but narrowly adaptive changes in nesting behavior.

Good examples of host-specific parasites are provided by members of the cuckoo-wasp genus *Parnopes*, several species of which have a wide distribution but are seldom abundant, perhaps because the sand wasps they attack have evolved nest closures sufficient to delay or prevent entry by the female parasites. In Jackson Hole, *P. edwardsii* is a parasitoid of *Steniolia obliqua* and probably of *Bembix americana spinolae* and *B. amoena*, the female digging through the nest closure to oviposit on the larva (Evans, 1966a). Chrysidids of the genera *Hedychrum*, *Hedychridium*, and *Ceratochrysis* were also found associated with certain ground-nesters (see Annotated List below), but the degree of host-specificity is not known.

¹ In fact, all of these are predators as that word is most commonly used. Like many entomologists, I use the word "parasite" loosely and here apply it to two kinds of associations: (1) parasitoids, which feed upon the host slowly and destroy it as they reach maturity; and (2) cleptoparasites, which feed principally upon the prey in the cell, but usually also kill the host larva. "Predators," as I use the word here, are also of two kinds: (1) those that capture and feed directly upon the prey, e.g., asilid flies; and (2) those that capture and paralyze prey and take it to the nest as food for the larvae, e.g., digger wasps.

The species of *Bembix* are also attacked by two apparently host-specific dipterous parasites: *Physocephala texana*, a conopid fly attacking the adults, and *Exoprosopa dorcadion*, a bee-fly that oviposits in open holes, its larva attacking the wasp larva. *Hoplisoides spilographus* and probably the species of *Gorytes* and *Dienoplus* are attacked by wasps of the genus *Nysson*, while various spider wasps are attacked by members of the cleptoparasitic pompilid genera *Ceropales* and *Evagetes*. (Records will be found in the Annotated List; for further details on these and related species see Evans and Yoshimoto, 1962, and Evans, 1966a.) This essentially completes the list of parasites that confine their attacks to a restricted group of hosts in this area. None of them are overly abundant in Jackson Hole, and there is no evidence from here or elsewhere that they cause profound depressions in the population sizes of their hosts.

Some of the non-host-specific parasites, notably the miltogrammine flies (Sarcophagidae), stand in strong contrast to these. These flies are abundant in virtually all areas inhabited by ground-nesting wasps in Jackson Hole as elsewhere. The most ubiquitous species is *Senotainia trilineata* (Fig. 10), often spoken of as a "satellite fly," since the females follow closely behind prey-laden wasps and larviposit upon the prey, often just as it is being taken into the nest. The small maggots typically destroy the egg of the wasp within a few hours after it is laid, then develop at the expense of the prey in the cell. Generally several maggots are deposited at once, and several (rarely up to 20) may develop successfully in one cell. In Jackson Hole, I have reared this fly from the cells of six species of Sphecidae, and altogether 17 species belonging to three families may be regarded as probable hosts (List 2). In fact, records from many localities suggest that these satellite flies follow wasps of many genera of several families and that their larvae develop suc-

cessfully in the nests of most species. However, in the case of maggots introduced by progressive-provisioners (such as *Bembix*) after the larva has begun to grow, the wasp larva and the maggots may both survive; I record one such case for *B. americana spinolae* and *Senotainia trilineata* below.

LIST 2

Hosts of *Senotainia trilineata* at Jackson Hole¹

EUMENIDAE

Stenodynerus p. papagorum (Viereck)*

POMPILIDAE

Episyron q. quinquenotatus (Say)**

SPHECIDAE

Aphilanthops subfrigidus Dunning*

Astata nubecula Cresson

Belomicrus f. forbesii (Robertson)

Bembix americana spinolae Lepeletier

Gorytes canaliculatus asperatus Fox*

Nitelopecterus evansi Krombein*

Oxybelus uniglumis quadrinotatus Say

Philanthus crabroniformis Smith

Philanthus pacificus Cresson*

Philanthus pulcher Dalla Torre*

Philanthus zebratus nitens (Banks)

Plenoculus davisii Fox**

Tachysphex nigrior Fox*

Tachysphex tarsatus (Say)**

Tachysphex terminatus (Smith)**

Two other satellite flies, *Hilarella hilarella* and *Taxigramma heteroneura*, were taken at MOR, the first associated with three unrelated species of Sphecidae, the second with two unrelated sphecids. I did not rear these flies from any nests and little is known of their biology, but I would assume that they are similar to *Senotainia*

¹ Reared from nests unless marked with an asterisk:

* Seen following females but not reared from cells;

** Known to be attacked on basis of studies elsewhere.

in their mode of attack and development, as well as in their lack of host-specificity.

The miltogrammine fly *Metopia argyrocephala* was reared from a nest of *Gorytes canaliculatus asperatus* and was found closely associated with the nests of five other sphecids. This fly also sometimes follows female wasps to their nests, but rather than larvipositing on the prey in transit, it enters the nest and larviposits in the cell. "Hole-searchers" such as this probably also locate open nests by random searching.

One of the most abundant Miltogramminae in Jackson Hole is *Phrosinella pilosifrons*, a relatively large fly with slightly expanded front tarsi that is often seen digging at closed nest entrances (Fig. 14). I have never observed this fly trailing female wasps or being attracted to open holes; rather it moves from one closed nest entrance to another where it now and then attempts to dig through the closure, when successful presumably larvipositing in the burrow or cell. Whether it is attracted to nests by the sight of fresh digging or by odor has not been determined. The maggots of *Phrosinella* are large, and usually one develops per nest cell (in a rearing tin one maggot may move to other cells and destroy them). In Jackson Hole, I found this species associated only with the species of *Philanthus*, and reared numerous flies from the cells of three species: *pulcher*, *crabroniformis*, and *zebratus*. However, other species of *Phrosinella* are known to attack a diversity of ground-nesters that maintain closures, and I would expect the same to be true of *pilosifrons*.

There is need for detailed field studies of these and other species of Miltogramminae, for these flies are unquestionably major pests of digger wasps and may have played an important role in molding various attributes of their nesting behavior, as discussed below. Despite various devious flight patterns, closures, accessory burrows, and so forth, the percentage of cells successfully attacked may be quite

high: about 20 per cent in *Philanthus zebratus nitens*, a species possessing several behavioral mechanisms evidently functioning to reduce the success of parasites. There is evidence that these flies sometimes cause marked decline in local populations of certain digger wasps.

Among the general predators at Jackson Hole should be mentioned asilid flies, including at least two species of *Laphria*, which tend to prey extensively upon Hymenoptera. These flies were often seen perching on logs or bushes overlooking nesting sites and dashing periodically at flying insects; one was taken with a sphecid wasp in its grasp, while others were seen with bees and sawflies. Spiders of many kinds also occur on the ground and in vegetation and probably take a considerable toll among the small wasps, although I obtained only one specific record of predation by a spider.

Finally, it should be remembered that four species of *Philanthus* prey upon wasps, two of them quite extensively. While the majority of wasps taken as prey are males, a good many females are also taken, including species nesting in close proximity to *Philanthus* (Lists 4 and 7). It is interesting to note that while Sphecidae, Eumenidae, Masaridae, Chrysididae, and even parasitic Hymenoptera appear on the lists of *Philanthus* prey, Pompilidae do not. Pompilids are certainly abundant at Jackson Hole both on the ground and on various flowers visited by *Philanthus*. Possibly their swift and erratic flight patterns render them difficult to capture. It should also be noted that in no case has a *Philanthus* been found to take another *Philanthus* (of any species) as prey, even though *zebratus* has been found to use the very similar and closely related wasp *Aphilanthops subfrigidus*. Although Rathmayer (1962) has shown that *Philanthus* is immune to its own venom, it seems more probable that these wasps are able to avoid attacking members of their own genus, perhaps by olfactory cues. This would be

an exciting problem to study experimentally.

SUMMARY OF INTERRELATIONSHIPS

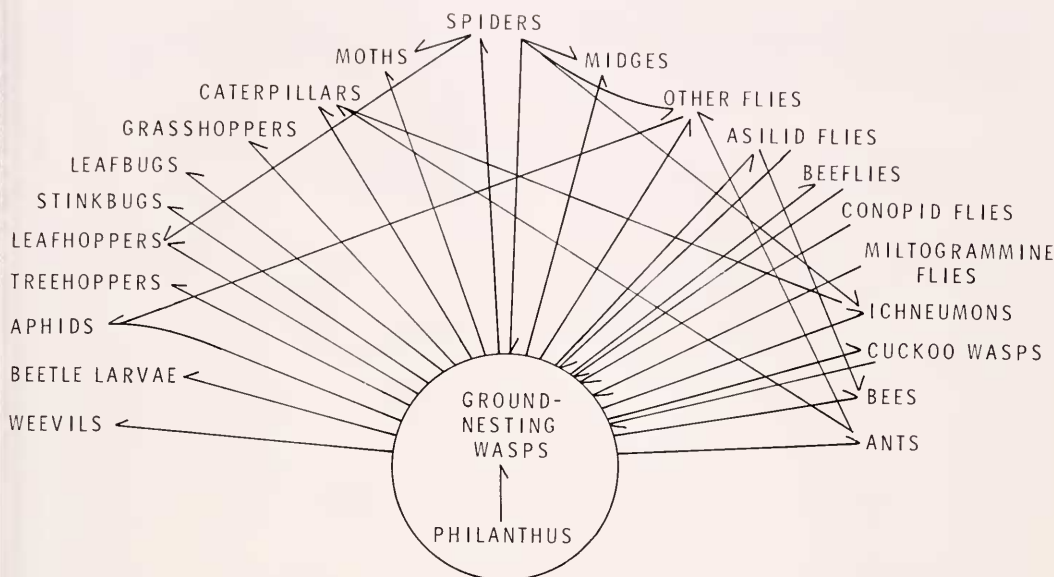
Digger wasp communities of Jackson Hole involve food webs that cannot adequately be summarized because of their complexity and because of shortcomings in our knowledge. The wasps are energetic predators that harvest great numbers of arthropods within and around their nesting sites. For example, if there were 50 nesting female *Bembix americana spinolae* at MOR-A2 and each prepared five nests containing 20 flies each (all highly conservative estimates), these wasps would have collected 5000 flies from the surrounding countryside. The aggregation of *Philanthus zebratus* at ELK contained an estimated 200 females, each of which prepared an estimated 15 cells provisioned with an average of about six prey; thus the members of this population must have collected at least 18,000 bees and wasps, evidently chiefly from flowers in the general vicinity of the nesting area.

Considering the abundance of ground-nesting wasps in certain areas and their efficiency as predators, it is not surprising that most species occupy different food niches. That some species do appear to prey upon the same arthropods during the same season may be attributable to: (1) the great abundance of such insects as aphids, leafhoppers, small halictid bees, etc.; and (2) the fact that virtually all wasps may maintain submaximal population sizes as a result of widespread parasitization, especially by miltogrammine flies. During seasons when, for climatic or other reasons, certain arthropods are unusually scarce, wasps which occupy similar food niches may be especially affected, and during seasons when one particular non-specific parasite is especially abundant, those species relatively unprotected against it may suffer profound population declines. Various short-range and long-range climatic factors may affect

predators, prey, and parasites differently, thus providing a continually changing environment which must be met by behavioral adjustments of one kind or another, or decline and local extinction may follow.

Some of these changes were obvious during the three summers I worked in Jackson Hole. In 1964, deerflies (*Chrysops*) were exceedingly abundant at MOR, and these flies were used as prey by *Bembix* almost to the exclusion of other flies. In 1967, doubtless as a result of a different rainfall or temperature pattern, deerflies were rarely in evidence, and the *Bembix* had shifted wholly to other flies (List 3). Some of these other flies provide the common prey of *Oxybelus* and of *Steniolia obliqua*. The latter species underwent a steady decline in numbers at MOR from 1961 to 1967. To what extent this has been due to competition for prey with *Bembix*, to success of its several parasites, or to changing climatic factors, is unknown. Since *Steniolia* often nests in the middle of paths and dirt roads, its decline may be largely the result of increasing numbers of humans and horses. Human interference may, in fact, be having an important influence on wasp populations even in this supposedly sacrosanct area. I suspect, for example, that construction of the Jackson Lake dam and resulting control of flooding along the Snake River may eventually diminish the alluvial deposits along the river. Sand bars have their own life cycles, and unless refreshed by wind or water eventually become overgrown and the soil greatly altered.

Even in the absence of human interference, changes in soil conditions and in vegetative cover are continually occurring, and these changes result in the expansion and contraction of suitable nesting space for certain species. It is difficult to evaluate such factors, as little is known of the precise edaphic relationships of wasp species. As in the case of food resources, it is probable that the abundance of natural



Text-figure 2. Diagrammatic representation of some of food relationships of wasps and their prey and parasites at Jackson Hole. Direction of arrow indicates direction of predatory or parasitic relationship (for energy flow, read arrows backward).

enemies ameliorates the intensity of competition for space; that is, many populations may be kept at levels sufficiently low that they do not fill all suitable nesting areas. At the same time, the need for bare, friable soil restricts many of these wasps to areas of loess or alluvium and thus pushes many species into close proximity. In these restricted areas, the build-up of non-specific parasites may play a major role in permitting such a diversity of species to co-exist (see, e.g., Paine, 1966).

I have attempted to delineate a few of the food relationships in the areas of study in Text-figure 2. Obviously, the arthropods used as prey by the wasps have other natural enemies, some of them in themselves serving as prey for wasps. The common orb-weaving spider *Araneus patagiatus*, for example, is the major prey of *Episyron quinquenotatus*, but itself preys on the small flies that provide the major prey of *Oxybelus* and *Crossocerus*. Thus an increase in the population of *Episyron* might permit an increase in the species of

the latter two genera. The Ichneumonidae preyed upon by *Philanthus zebratus* are parasites of caterpillars, some of which may serve as prey of *Ammophila* and other wasps. Thus a high population of *Philanthus* might favor such a wasp as *Ammophila azteca*—except that, ironically, *P. zebratus* also preys directly upon *Ammophila*. *P. pulcher* preys upon cuckoo wasps to some extent, including species known to attack other ground-nesting wasps. The species of *Philanthus*, indeed, provide the most interesting elements in this fauna, preying as they do on so many wasps, wasp parasites, and parasites of other insects—also, of course, on many bees, which to a certain extent compete with wasps for nesting sites and nectar sources.

Insufficient information is available to explore these interrelationships further—in fact, I have already gone farther than the data warrant—and I should like to turn to the second question posed at the beginning of this section: to what extent

are species differences in behavior understandable in the contexts of interspecific competition and of widespread parasitization?

BEHAVIOR PATTERNS AS ADAPTATIONS TO LIFE IN THE COMMUNITY

There exists a very extensive literature describing the behavior patterns of solitary wasps, for it is true that these patterns are subject to relatively little intraspecific variation and that species differences, even between closely related forms, are often pronounced. However, few attempts have been made to explain these different behavior patterns in terms of their adaptive value. Why do related species often show pronounced differences in prey preferences, manner of approach to the nest, nest closure, mound-leveling, accessory burrows, and so forth? In my opinion the two factors emphasized here—competition and parasitism—are sufficient to explain the adaptive value of nearly all of the species-specific behavior patterns of solitary wasps (see also Evans, 1966a, Chapter XV).

BEHAVIOR RELATED TO COMPETITION¹

The relatively high degree of ecological displacement among the wasps of Jackson Hole is by no means a unique phenomenon; a very similar picture is presented by the solitary wasps of eastern Massachusetts, for example. Indeed, that ecological homologues cannot coexist is a widely recognized biological phenomenon (DeBach, 1966).

¹ It may be argued that neither food or nesting sites have been shown to be in short supply, and thus competition cannot be demonstrated. But, as pointed out in this section, speed is important to these short-lived insects, and if two species prey on the same thing or nest in the same place, any interference or diminution in space or in the numbers of prey which lengthens their nesting cycles will result in a reduction in number of offspring. I use the word "competition" in this broad sense, to include any interspecies rivalry that is selectively disadvantageous (see also DeBach, 1966).

There are no well-documented exceptions among the wasps of Jackson Hole, for those few species appearing to have identical or broadly overlapping food niches occupy different nesting sites—and this in itself suggests that they may hunt in somewhat different areas. Obviously several sets of behavior patterns are involved here: selection of a nesting site; construction of a nest compatible with that soil type; selection of a hunting site; and response to a particular kind of prey.

No studies were made of hunting behavior, but it can be assumed that even slight differences in prey selection involve important differences in responses to stimuli. A given species of wasp may be narrowly or fairly broadly adapted with respect to prey selection. *Aphilanthops subfrigidus*, which (like its congeners) preys only on queen ants of the genus *Formica* during their nuptial flights, must have highly specialized hunting behavior indeed. On the other hand, *Bembix americana spinolae* is known to forage widely and to respond to Diptera of various shapes and sizes—including such diverse flies as asilids, tabanids, and sciomyzids. *Aphilanthops* has the advantage of being the only wasp in this area using *Formica* ants as prey, but the success of these wasps is very much tied up with the size of nuptial flights and weather during such flights. *Bembix* uses large numbers of deerflies (*Chrysops*) when these are plentiful (a prey not known to be used by other wasps in this area), but when they are not in abundance it is readily able to utilize small muscoids (a common prey of *Oxybelus*) or bee flies (the almost exclusive prey of *Steniolia*). Such a broadened response to potential prey may have evolved in an area where there were fewer species of digger wasps and no competitors for larger flies. Under conditions of severe competition, one would expect a narrowing of the spectrum of response, perhaps at first non-genetic but later becoming fixed in a local population. Under conditions of prolonged

isolation, such a population might emerge as a species with restricted prey preferences.

There is evidence that various species of *Bembix* show differences in prey type in various parts of their ranges, though to what extent this is genetically determined is unknown. The same is true in *Philanthus*. *P. pacificus*, for example, has been studied at Antioch, California, and found to prey upon wasps and bees in approximately equal numbers, also on parasitic Hymenoptera such as Braconidae and Ichneumonidae (Powell and Chemsak, 1959). *P. crabroniformis* has been observed at Delta, Utah, capturing honeybees at the hive entrances (under the name *flavifrons* Cresson; G. E. Bohart, 1954). Both of these species prey very largely on small halictid bees in Jackson Hole.

It should be pointed out that the success of a predatory wasp is very much dependent upon the speed with which it is able to find and capture prey; if it is forced to search for an uncommon prey or to subdue an unusual prey, the result will be that during its limited lifetime each female will have time to provision fewer cells than usual. This being true, there will be great selective advantage in finding and capturing a particular kind of prey quickly, that is, toward more specialized hunting behavior. My observations on *Steniolia obliqua* hunting beetles (Evans and Gillaspay, 1964) suggest that it is a much more effective predator on these swiftflying Diptera than is *Bembix*. Thus *Bembix* may be at a disadvantage if forced to rely heavily on beetles in an area where a specialist on beetles, *Steniolia*, is abundant.

As already pointed out, related wasps seldom nest in identical sites. This results in a partitioning of available space and also tends to disperse aggregations of different species such that their hunting arenas are at least partially separate. Occupation of different soil types also influences the type of nest. Species nesting in highly friable,

dry sand tend to make a series of separate nests, often with one or a few cells; presumably such nests are less amenable to wholesale destruction by parasites than nests in which many cells arise from a single burrow. But in hard-packed, stony soil this presumed advantage is outweighed by the problems of digging. That is, it is advantageous for a species such as *Philanthus crabroniformis* to make a single burrow and ultimately to prepare many cells from it, even though such a nest may be more subject to parasitization by cuckoo wasps or *Phrosinella* flies than a more temporary nest with only a few cells. The female *Philanthus crabroniformis* requires several days to dig her burrow, while *P. pacificus* may complete a burrow in a sand bar in a few hours. The first species usually nests from a single burrow throughout its life, making fifteen or more cells (Fig. 38), while the second prepares a series of shallow nests, each with about three cells (Fig. 35). The correlation between soil texture and number of cells per nest is by no means absolute, but it is true that most of the nesters at MOR-B made multicellular nests (e.g., *Astata nubecula*, two species of *Eucerceris*, and *Belomicrus forbesii*) although a few prepared cells from pre-existing burrows (*Cryptocheilus terminatum*, and *Pisonopsis clypeata*). Here again, speed of work is important to a wasp living only a few weeks, and those species nesting in relatively intractable soil have evolved mechanisms for reducing the total amount of digging that must be done.

BEHAVIOR RELATED TO PARASITISM

I include here all behavior that appears to function in reducing the success of natural enemies. It is, of course, possible to consider these behavioral devices also as a form of competition. Crombie (1947) remarks that "agencies such as predators may produce a different kind of competition rather than preventing it altogether. They may, for instance, prevent compe-

tition for food among their hosts, but cause them to compete to avoid the predators, e.g., there may be selection for reflexes which assist this." I would agree with this statement, but nevertheless feel that it is useful to distinguish between direct interspecies competition and the competitive success of various species in reducing the attacks of natural enemies.

For example, prey selection is evidently related to interspecies competition, since it results in a partitioning of the available resources, as already pointed out. However, the manner in which the prey is carried to the nest has apparently evolved in response to parasite pressure, as I have argued elsewhere (Evans, 1963a). Jackson Hole has many wasps that carry the prey with their mandibles, but these wasps must either deposit the prey while they open the nest, thus rendering the prey temporarily unprotected against satellite flies, tiger beetles, ants, and so forth; or they may simply leave the nest open, making it available to beeflies, hole-searching miltoigrammine flies, and so forth. Jackson Hole also has many species that carry the prey with their middle legs, where it is well protected beneath the body and where it remains while the nest entrance is opened with the front legs. Only one species in this area carries the prey on the end of its abdomen, but that is one of the commonest species, *Oxybelus uniglumis quadrinotatus*. This species is a very rapid provisioner, and I assume speed has been selected for at the expense of exposing the prey to satellite flies.

Two of the larger species of *Philanthus*, both heavily attacked by *Senotainia* flies, exhibit strikingly devious flight patterns upon approaching their nest with prey. In the case of *P. crabroniformis*, prey-laden females (whether or not followed by satellite flies) almost always fly not directly to the nest but to a low herb or grass blade 0.5–2.0 m from the entrance. Here they often cling for a few seconds before proceeding to another perch or (if no flies are

present) to the nest. Once at the entrance, females almost always dig through the closure and enter, even though a satellite fly may have appeared in the meantime. Some females followed by flies move about from perch to perch (always within 20 cm of the ground) at varying distances from the nest for as long as five minutes before entering. On several occasions females were seen to lose their would-be parasites before reaching the nest.

The corresponding flight patterns in *P. zebhratus* differ in some details. These wasps, with their generally rather large prey, typically descend into the nesting area from a considerable height, landing with an audible sound on the ground and sitting motionless for several seconds before continuing to the nest. If followed by satellite flies, they fly off close to the ground in a circuitous pattern, often disappearing from sight for several seconds to a minute or two. This may be repeated several times if the flies persist or reappear. Although prey-laden females may land on the ground occasionally, they seldom land on vegetation in the manner of *crabroniformis*. Some females followed by flies rise high in the air and descend abruptly as in their initial return flight.

These two species of *Philanthus* are also the only wasps in Jackson Hole known to maintain accessory burrows. These short burrows are dug beside the true burrow and are left open while the true burrow is closed. In *crabroniformis*, a nester in hard soil, newly completed nests lack an accessory burrow, but as females replace their closures again and again they often scrape much of the soil from small quarries beside the nest entrance, so that within a few days numerous nests have such quarries, later in the season still more. For example, on August 3, I counted 26 nests, of which four had one quarry each. On August 12, a count of 40 nests (including all of the original 26) showed that about half had quarries, several of them two (one on each side or both on one side). The quar-

ries varied in depth from 2 mm to 2.5 cm. Females were often seen entering the quarries and occasionally remaining within them for a few seconds. Their primary function was unquestionably as a source of fill in this hard soil. I did not observe any parasites being attracted to them, although it is probable that this sometimes occurs (for a general discussion of accessory burrows, see Evans, 1966b).

P. zebratus nests in much more friable soil, yet some females appear to quarry much of the sand for closure at one or two points, creating short accessory burrows which may be redug from time to time. On August 2, I estimated that 20 per cent of the nests had accessory burrows, and there was no evidence of an increase as the season progressed. Actually, about half of these nests had two such burrows, and several had three. They varied from barely measurable to 3 cm in depth. On three occasions hole-searching flies, *Metopia argyrocephala*, were seen entering these accessory burrows. It seems probable that in *zebratus* the burrows serve a more important role in diverting parasites, than as a source of soil.

These two species of *Philanthus* do not level the mound of soil at the nest entrance, merely leaving it in a fan-shaped pile. In contrast, mound-leveling behavior following completion of a new nest is elaborate in *P. pulcher* and *pacificus*. Mound-leveling behavior is also elaborate in *Bembix americana spinolae*, although absent in the related wasps *B. amoena* and *Steniolia obliqua*. In *Ammophila azteca* and other species of this genus quite another method of removing soil from the edge of the burrow is employed: the female carries small loads forward in flight and drops them some distance away. A variation on this "soil-carrying" theme is employed by *Belomicrus forbesi*, the females of which fly swiftly backward from the nest, each time carrying a lump of earth and dropping it on the ground.

It is assumed that removal of the soil

from the nest entrance renders the site less evident to parasites (as it does to humans). Cuckoo wasps and *Phrosinella* flies are often seen flying from one nest entrance to another, landing on the mound of soil and searching about for covered holes. They will also alight, at least briefly, on artificial piles of sand placed in nesting areas, suggesting that their initial attraction is to the sight of the mounds.

Closure of the nest entrance between hunting flights is also regarded as a device for rendering the nest less visible and also for delaying or preventing the entry of diggers such as *Phrosinella* or *Parnopes*. This belief is supported by observations and simple experiments. Bombyliid flies oviposit into many kinds of holes, including artificial holes made by a pencil in the soil. *Metopia* flies also enter various open holes, including blind accessory burrows, as mentioned above. There is, however, a paradox here: *Phrosinella* evidently is not attracted to open holes, but only to closed nests (though presumably preferring thin closures to thick ones); and *Senotainia* is favored by closures, since they cause the wasps to pause at the entrance to dig it open and thus provide a better target for larviposition. The fact that the vast majority of the fossorial wasps of Jackson Hole do maintain a closure suggests that these factors are generally outweighed by others, that is, when and where closing behavior evolved *Senotainia* was a less important parasite than some others. The apparent success of *Phrosinella pilosifrons* against *Philanthus* may reflect the fact that although these wasps do close the nest, the closure is usually rather weak.

The species of *Tachysphex* ought to provide unusually good material for a study of the influence of closure on success of parasites, especially since the nests are shallow and easy to excavate. One would assume that the species making no closure (*tarsatus* and *nigrior*) might be more heavily parasitized by *Metopia* and less heavily parasitized by *Senotainia* than the

species that make a closure (*terminatus* and sp. nr. *linsleyi*). On the other hand, the fact that the first two species use relatively larger grasshoppers, which protrude further behind their bodies in transit, may mean that they present a better target for satellite flies, thus offsetting the advantage of quick entry into the nest. Unfortunately, none of the species of *Tachysphex* are abundant in Jackson Hole.

The digger wasps that omit the outer closure include several that make vertical burrows. Such burrows cannot be closed in the usual manner of simply scraping soil into the entrance; either they must be left open, or special mechanisms evolved. The species of *Eucerceris* leave the entrance open, but possibly compensate for this by keeping a certain amount of loose sand in the lower part of the burrow. *Stenodynerus papagorum* makes a vertical burrow, but in this case it is capped by a mud turret (Fig. 23). These turrets may have evolved as deterrents to parasites, but I have seen cuckoo wasps entering them, and Olberg (1959) has provided a photograph of a cuckoo wasp entering the turret of a different species. Although the species of *Ammophila* make short, vertical burrows, they have evolved unique behavior enabling them to close their burrows effectively. Briefly, the female finds an object that just fits the lumen of the burrow, fits it in place, then puts additional lumps and loose soil above it (Fig. 31).

Final closure of the nest in *Ammophila azteca* is also enhanced by the "tool using" behavior of this species, which surely serves to provide a firm barrier against parasites and to form a plug which does not erode and expose the location of the shallow nest to predators. Many other wasps make a fairly lengthy final closure (*Bembix americana spinolae* and *Philanthus pulcher*, for example), but whether the species of *Philanthus* that nest in one burrow for their entire lives usually fill up the burrow before they die is doubtful.

Progressive feeding of the larva probably

also arose in response to parasite pressure (Evans, 1966a). In Jackson Hole, *Ammophila azteca*, *Bembix americana spinolae*, and *Steniolia obliqua* are the only known progressive provisioners. Since these wasps require five days or more to complete a single cell (as compared to usually about one day for mass provisioners), they would seem to be at a disadvantage when the seasons are as short as they are here. The three may thrive simply because almost none of the larvae succumb to parasites; as noted above, miltogrammine fly maggots and wasp larvae may both survive in such nests, at least at times. *Ammophila azteca*, furthermore, has evolved an unusual behavioral feature peculiarly adaptive for these short summers: successive nests overlap, the female maintaining two to four nests at different stages of development and remembering the location of each (Evans, 1965).

Admittedly the success of these various behavioral devices has yet to be documented quantitatively. In fact, it is uncertain whether it can be, both because of the difficulty in obtaining such data for ground-nesting species and because the data, if obtained, may not mean a great deal. The parasites and their hosts have undoubtedly undergone a measure of co-evolution, and if a particular behavioral device does not seem effective, it may mean that the parasites are, at this stage, "one step ahead."

SUMMARY OF BEHAVIORAL ADAPTATIONS

No two of the wasp species studied in Jackson Hole are behaviorally alike in every respect. This suggests that each has evolved to meet somewhat different problems. There is no way of knowing where or when these distinctive patterns evolved. The present is the only time-transect we have, and the interplay among the various members of the fauna today can only suggest some of the problems these species have surmounted. At least in this context many otherwise puzzling behavior patterns

"make sense." Our explanations may not be complete, or even correct, but at least they provide the basis for a fuller understanding of the biological role of each species attribute than any amount of study of museum specimens is likely to provide.

In these restricted areas of bare, friable soil in Jackson Hole—and in similar areas elsewhere—a wasp must have certain behavioral capabilities in order to be successful. Some of these are as follows:

(1) It must hunt prey which is readily available and not overly exploited by other predators, and its hunting behavior must be closely attuned to the habitat and behavior of that particular prey.

(2) It must utilize available sources of nectar or honeydew for its own nourishment without undue interference or over-exploitation of the source by bees or other wasps.

(3) It must nest where there is available space not densely filled with other wasps or with ground-nesting bees, and it must construct a nest appropriate to that soil type.

(4) It must be able to provision its nest quickly and with a minimum of delay due to prey scarcity or to interference from other wasps or from parasites, especially in an area with a short summer season.

(5) It must possess mechanisms for reducing the success of parasites to such an extent that each female is able to leave at least two progeny that survive to adulthood. Examples of such mechanisms include pedal prey carriage, devious flight patterns, nest closure, mound leveling, accessory burrows, progressive provisioning, and so forth.

Possession of these attributes in various forms—and, of course, such other obvious ones as the ability to survive the winters at this latitude and altitude—has enabled these species to coexist, some with greater success than others. Paradoxically, it may be the presence of so many natural enemies that permits so many species to occur to-

gether, as discussed earlier; yet each species appears committed to evolutionary strategies for incurring a lessened incidence of successful attack by these enemies.

It may be instructive to summarize these strategies for the species of one genus. *Philanthus* has five species in Jackson Hole, and, by coincidence, five common species in eastern Massachusetts (all different). Eventually I hope to complete a detailed comparative study of these ten species, but for the present I offer a tabular comparison of some of the more salient attributes of each (Table 1). In each area there are certain species in which mound-leveling is well developed (all of these are members of the *politus* species-group). In each area there are species in which accessory burrows are sometimes constructed, and in the eastern states one (*lepidus*) in which such burrows form a fixed feature of behavior (although varying in number). All Jackson Hole species make a nest closure, but two eastern species omit the closure. Such differences presumably reflect the relative importance of satellite flies, beeflies, and other natural enemies at the times and places when these behavior patterns evolved; e.g., open nest entrances permit rapid entry and may reduce the success of *Senotainia*, while permitting access to the nest by *Metopia*, bee-flies, etc. Others (prey type and soil type, also size, time of emergence, and other qualities not tabulated here) probably represent mechanisms for reducing direct competition with congeners. A similar analysis of other genera would provide a very similar picture.

It is obvious that the functional significance of these various behavior patterns remains unproved. The conclusions I have drawn are based on extensive field work in Jackson Hole and elsewhere, but I would be the first to admit the need for many more observational data, for experiments designed to test critical points, and for mathematical approaches such as those of many contemporary population biologists.

TABLE I
COMPARISON OF TEN SPECIES OF *Philanthus* WITH RESPECT TO SIX BEHAVIORAL FEATURES.

Species	Nest type ¹	Soil type ²	Prey type ³	Levels mound at entrance	Temporary closure	Accessory burrows
Jackson Hole, Wyoming						
<i>pacificus</i>	S	1	SB	+	+	0
<i>pulcher</i>	S	2	BW	+	+	0
<i>crabroniformis</i>	P	3	SB	—	+	0-2
<i>zebratus</i>	P	2	BW	—	+	0-3
<i>bicinctus</i>	P	3	LB	—	+	0
Eastern Massachusetts						
<i>politus</i>	S	1	SB	+	+	0
<i>gibbosus</i>	P	2	SB	—	+	0-2
<i>lepidus</i>	S	1	SB	—	+	1-5
<i>solivagus</i>	P	1a	BW	—	—	0
<i>sanbornii</i>	P	2	LB	—	—	0

¹ Nest type: S—a succession of simple nests with few cells.

P—a more or less permanent, multicelled nest.

² Soil type: 1—light, fine-grained sand; 1a—such sand, but only on slopes.

2—coarse, moderately friable sand.

3—very coarse-textured sandy gravel.

³ Prey type: SB—small bees; LB—large bees; BW—both bees and wasps used in numbers.

The complexity of these communities is such that they must be examined from many points of view. A behavioral adjustment on the part of one species, or the extinction of a species or arrival of a new one—or, indeed, the varying population sizes of each species belonging to the community, even peripherally—each of these factors may have subtle effects upon many members of the community. Hence no factor, no behavior can a priori be regarded as unworthy of study. The twin sciences of ecology and ethology are certain to become increasingly important with our growing concern with the environment and our growing awareness of its complexity. Despite welcome advances in theory and the promise of computerization, it appears that the need is greater than ever for what is sometimes called “old fashioned natural history.”

ANNOTATED LIST OF WASPS OF JACKSON HOLE

The following is a list of wasps collected in the areas of study, with a brief summary of their nesting behavior, if known. Arrangement of families and genera is the

conventional one, approximating that in the Second Supplement of the Synoptic Catalog of North American Hymenoptera (Krombein and Burks, 1967). A few species taken outside the immediate area of study are included but are enclosed in brackets. The major localities were described earlier (see “Study Areas”), but the abbreviations used are repeated here for the sake of ready reference:

ELK: 4 miles SW of the Elk Post Office (Map 1);

HHS: Huckleberry Hot Springs, Teton National Forest;

JAC: 5 miles north of Jackson;

MOR: Moran, near Jackson Hole Research Station (Map 1);

MOR-A: Largely restricted to alluvial sand;

MOR-B: Chiefly in bare places in lower outwash plain;

PCR: Pilgrim Creek, 4 to 7 miles NE of Moran.

Records of adults feeding on the nectar of flowers are also included, and again several abbreviations have been employed:

Eri: *Eriogonum* spp. (wild buckwheat);

Per: *Perideridia gairdneri* (yampa);

Sol: *Solidago* spp. (goldenrod);

Several species were taken in Malaise traps set up in MOR-A1, but not elsewhere. These are identified simply by the word "trap."

The insect fauna of Jackson Hole is by no means thoroughly known, and in a number of cases I have been able to identify wasps only to genus. Some species identifications may prove incorrect as the systematics of Hymenoptera improves. However, all material collected has been placed in the collections of the Museum of Comparative Zoology, and specimens with associated behavioral data are cross-referenced by number to my field notes, also on permanent file at the Museum. Thus, if problems arise regarding the identity of any of the species studied, it should be possible for specialists to re-examine this material.

I identified many of the wasps myself, but received valuable help from several persons, especially from R. M. Bohart (Chrysididae, Eumenidae, and certain Sphecidae), A. S. Menke (*Ammophila*), F. D. Parker (*Astatinae* and *Leptochilus*), F. E. Kuczewski (*Tachysphex*), and K. V. Krombein (various Sphecidae). Most of the prey were identified by various specialists located at the U. S. National Museum, but H. W. Levi identified the spiders, and H. J. Reinhard and F. C. Thompson assisted with the flies. P. H. Timberlake undertook the arduous task of identifying the many bees taken as prey by species of *Philanthus*.

Family DRYINIDAE

These small wasps are parasites of leafhoppers and plant hoppers; they make no nest but leave the prey on vegetation, where it recovers from paralysis and continues feeding. The American species have been little studied, and species identification is nearly impossible.

Chalcogonatopus sp. MOR, July 28–Aug. 15, 1 ♀, 2 ♂♂.

Anteon sp. MOR, July, 1 ♂ in trap.

Aphelopus comesi Fenton. MOR, Aug., 1 ♂ in trap.

Family CLEPTIDAE

Cleptids have been reared from sawfly larvae. Only one species has been taken in Jackson Hole.

Cleptes provancheri Aaron. MOR, July 11–Aug. 16, 5 ♀♀, 1 ♂, ♀ on Per, one ♀ in trap; PCR, Aug. 2, 1 ♀, 1 ♂.

Family CHRYSIDIDAE (Cuckoo wasps)

Cuckoo wasps are parasites of various wasps and bees, usually entering the nest and laying their egg while the host is absent. A good recent account of several species is provided by Krombein (1967). Although cuckoo wasps are abundant in Jackson Hole both in individuals and in numbers of species (24), I obtained no important new information regarding their biology.

Omalus aeneus (Fabricius). MOR-B, July 6–30, 1 ♀, 2 ♂♂; note no. 1981: 1 ♀ taken from a nest of *Philanthus pulcher*, as prey. This wasp is known to parasitize species of *Passaloecus*, *Pemphredon*, and *Stigmus* nesting in cavities in wood.

Omalus plicatus (Aaron). MOR-B, Aug. 1, 1 ♀.

Omalus purpuratus (Provancher). MOR-A, July, 2 ♀♀, in trap.

Omalus speculum (Say). MOR, July 28–Aug. 1, 1 ♀, 1 ♂.

Omalus variatus (Aaron). MOR, July 19–Aug. 13, 1 ♀, 2 ♂♂; ELK, July 10, 1 ♀.

Elampus viridicyaneus Norton. MOR, July 11–Aug. 3, 5 ♀♀; JAC, July 15, 2 ♀♀. Note no. 2110B; 1 ♂, MOR-B3, taken from nest of *Philanthus pulcher* as prey.

Holopyga hora Aaron. MOR, July 16–30, 2 ♀♀.

Holopyga ventralis (Say). MOR-B, July 11–Aug. 11, 2 ♀♀, 4 ♂♂, ♀♂ on Sol, Per; ELK, Aug. 4, 1 ♂; PCR, Aug. 2, 1 ♀. Note no. 1981: 1 ♀, MOR-B3, taken from nest of *Philanthus pulcher*, as prey.

Hedychridium fletcheri Bodenstein. MOR, July 11–Aug. 23, 8 ♀♀, 4 ♂♂; ELK, Aug. 4, 1 ♂; HHS, July 17, 1 ♂. Note nos. 1981, 1984, 2118: 1 ♀, 3 ♂♂, MOR-B3, taken from nests of *Philanthus pulcher*, as prey. Note nos. 2096, 2109: 2 ♀♀, both taken on ground in *P. pulcher* nesting areas, MOR-B3, July 14, 21, 1967.

These females were flying from one nest entrance to another, apparently attracted by the fresh earth at the entrances. They were not seen to enter any nests (other wasps and various bees were also nesting here). The species of this genus apparently attack ground-nesting wasps; *H. fletcheri* is reported to attack *Tachysphex*, while some European species are said to attack *Dienoplus* spp.

Hedychrum nigropilosum Mocsary. MOR, Aug. 1, 1 ♂.

Hedychrum parvum Aaron. MOR, July 16–Aug. 14, 1 ♀, 3 ♂♂, ♂ on Per. Note no. 2048: ♀ found in burrow of *Eucerceris fulvipes* Cresson while I was digging out nest, Aug. 14, 1964, MOR-B1. Since other species of this genus are known to attack *Cerceris* spp., it seems probable that this individual was in fact attacking *E. fulvipes*.

Chrysura densa (Cresson). MOR, July 6, 1 ♂; Death Canyon, Aug. 15, 1 ♀.

Chrysura pacifica (Say). JAC, July 15, 1 ♀; MOR, July 4–16, 3 ♀♀, 2 ♂♂, 1 ♂ no. 1981: taken as prey by *Philanthus pulcher*.

Ceratochrysis cyanosoma (Mocsary). MOR, Aug. 26, 1 ♀.

Ceratochrysis perpulehra (Cresson). MOR, July 13, 1 ♀; PCR, Aug. 2, 1 ♀.

Ceratochrysis trachypleura Bohart. MOR, July 20–Aug. 26, 11 ♀♀, 3 ♂♂; ELK, July 28, 1 ♀; HHS, Aug. 11, 1 ♀. Note nos. 1996, 2109, 2135, all MOR-B, July, Aug.

Several females were seen landing at nest entrances and walking over soil at entrances, but not entering; nests were those of *Philanthus pulcher*, *P. crabroniformis*, and *Ammophila azteca* (cuckoo wasp erroneously identified as *Ceratochrysis perpulehra* in my 1965 paper on *A. azteca*). This species is common in Jackson Hole and is surely a parasite of one or more species of ground-nesting wasps or bees, but I have no evidence as to which ones. *C. perpulehra* is reported as a parasite of *Ammophila aberti*, but the type species of the genus, *enhuyeki* Cooper, is a parasite of the twig-nesting eumenid *Leptochilus*. There are two distinct color forms of female *trachypleura* in Jackson Hole, one blue-green, the other with a strong overlay of coppery and rose tints; the two are represented in about equal numbers.

Trichrysis doriae (Gribodo). MOR, July, Aug., 3 ♀♀, in trap.

Chrysis coeruleans Fabricius. MOR, July 11–Aug. 15, 9 ♀♀, 1 ♂, several in trap; ELK, Aug. 4, 1 ♂; PCR, Aug. 2, 1 ♀. This species attacks various twig-nesting Vespidae; Krombein (1967) has recently discussed its biology.

Chrysis derivata Buysson. MOR-A, July, 1 ♀, in trap. Also known to be a parasite of twig-nesting Vespidae.

Chrysis dorsalis Aaron. MOR-B, Aug. 1–26, 3 ♀♀, 1 ♂, ♀♂ on Per.

Chrysis pattoni Aaron. MOR, July 7, 1 ♂; HHS, July 17, 1 ♀.

Chrysis snowi Viereck. MOR, July 16, 1 ♂.

[**Chrysis stenodyneri** Krombein. South Gate, Yellowstone National Park, July

19, 1 ♀. This species and *pattoni* are both reported to attack twig-nesting Vespidae.]

Chrysis venusta Cresson. MOR-A, July 16–Aug. 3, 2 ♀♀. Note no. 2108: 1 ♀, seen entering the mud turret at a nest of *Stenodynerus papagorum* and coming out again within a few seconds. It is possible that this species attacks ground-nesting rather than twig-nesting Vespidae.

Parnopes edwardsii (Cresson). MOR-A, July 18–Aug. 26, 17 ♀♀, 2 ♂♂; ELK, Aug. 4, 1 ♀; HHS, July 17, 1 ♀. Note nos. 1819, 1987, 1997, MOR: females commonly seen in the nesting sites of *Stenolia obliqua* and *Bembix americana spinolae* (and observed digging into nests of the former species). This is a known parasite of *S. obliqua* and *B. americana comata*, and is a probable parasite of other Bembicini (for details see Evans, 1966a).

Family SIEROLOMORPHIDAE

Nothing is known of the biology of these wasps. One species is common in Jackson Hole, and is usually collected by sweeping low vegetation in sandy places.

Sierolomorpha nigrescens Evans. MOR, July 12–22, 1 ♀, 16 ♂♂.

Family TIPHIIDAE

Only four species of this large family have been taken in Jackson Hole, all on sandy soil near the Snake River.

Tiphia sp. near **essigi** Allen. MOR, July 29–Aug. 11, 4 ♀♀, 3 ♂♂, ♀♂ on Per; ELK, Aug. 4–10, 5 ♂♂. Species of this genus are parasites of white grubs (Scarabaeidae).

Tiphia infossata Allen. MOR, July 12, 1 ♀.

Methocha stygia (Say). MOR-A, July 16, 1 ♀. Species of this genus attack the larvae of tiger beetles in their burrows

in the soil. The single female taken in Jackson Hole has a dull, striate thoracic dorsum like other females from the northwestern states and western Canada. It is possible that these will prove specifically or subspecifically distinct from *stygia*.

Myrmosa unicolor Say. MOR, July 11–24, 1 ♀, 3 ♂♂, 2 ♂♂ in trap. This wasp has been reared from cocoons of *Tiphia*.

Family MUTILLIDAE (Velvet ants)

The two species of mutillids occurring in Jackson Hole are both relatively uncommon; both may be parasitic on ground-nesting bees.

Dasymutilla myrice Mickel. JAC, July 25, 2 ♂♂.

Dasymutilla fulvohirta (Cresson). MOR, Aug. 17–26, 2 ♂♂; JAC, July 25, 1 ♂.

Family SAPYGIDAE

Sapygid wasps are parasites of bees. I have taken only two specimens in Jackson Hole.

Eusapyga rubripes proxima (Cresson). MOR, July 16, 1 ♂.

Sapyga confluenta Cresson. MOR, July 30, 1 ♀.

Family EUMENIDAE (Mason wasps)

These wasps carry water to moisten dry soil, the resulting pellets being used to make free mud nests, to partition off cells, or to build mud turrets. All species use eruciform larvae as prey and oviposit in the empty cell before prey is brought in. In Jackson Hole, I have collected 24 species, but only one of these, *Stenodynerus papagorum*, nests in numbers in the soil in the study areas.

Eumenes crucifera nearecticus Bequaert. MOR, July 29–Aug. 26, 2 ♀♀, 5 ♂♂, ♀♂ on Sol. This species, like the follow-

ing two, makes mud pots attached to twigs and provisions with caterpillars. I found no *Eumenes* nests in Jackson Hole.

Eumenes iturbide pedalis Fox. MOR, July 20, Aug. 12, 1 ♀, 1 ♂.

Eumenes verticalis coloradensis Cresson. MOR, July 8–Aug. 14, 3 ♀♀, 7 ♂♂; PCR, Aug. 2, 1 ♂; JAC, July 25, 1 ♀; Death Canyon, Aug. 15, 1 ♀.

Odynerus dilectus Saussure. JAC, July 15–25, 1 ♀, 1 ♂. This species is known to be a ground-nester and to surmount its burrow with an erect turret up to 2 cm high (Linsley and Michener, 1942).

Pseudepipona herrichii aldrichi (Fox). MOR, July 14–Aug. 23, 4 ♀♀, 2 ♂♂, ♀ on Sol.

Euodynerus auranus (Cameron). MOR, July 29–Aug. 3, 1 ♀, 1 ♂, ♂ on Sol.

Euodynerus castigatus (Saussure). MOR, Aug. 17–26, 1 ♀, 2 ♂♂, ♀ on Per, ♂ on Sol; ELK, Aug. 4, 1 ♂, note no. 2032: taken as prey of *Philanthus zebratus nitens*. Evidently the nest of this species has not been described. I have taken the liberty of including a photograph of a five-celled mud nest found under a stone in a field near Ithaca, N. Y. (note no. 1144; Fig. 22); several adults were reared from this nest.

Euodynerus f. foraminatus (Saussure). Death Canyon, Aug. 15, 1 ♂. Nests in hollow twigs (see especially Krombein, 1967).

Euodynerus leucomelas (Saussure). MOR-B, July 8–Aug. 26, 2 ♀♀, 1 ♂, ♀ on Sol; HHS, Aug. 11, 1 ♂. Also a twig-nester.

Euodynerus tempiferus eldoradensis (Rohwer). JAC, July 15, 1 ♀.

Ancistrocerus adiabatus (Saussure). MOR, July 20–Aug. 10, 3 ♀♀, 2 ♂♂, ♂ on Sol; HHS, July 17–30, 5 ♂♂; PCR, Aug. 2, 2 ♂♂; ELK, Aug. 4–21, 2 ♀♀,

1 ♂, note nos. 2132, 2133 (1 ♀, 1 ♂); taken as prey of *Philanthus zebratus nitens*. All but two females are of the white-banded color form called *alboluteus* by Bequaert.

Ancistrocerus a. antilope (Panzer). MOR-B, July 18–Aug. 26, 4 ♂♂, on Sol, Eri; PCR, Aug. 13, 1 ♂. This widely distributed twig-nester has been studied by Cooper (1953), Krombein (1967), and others.

Ancistrocerus c. catskill (Saussure). MOR-B, July 5–Aug. 26, 7 ♀♀, 10 ♂♂, ♀♂ on Sol, Eri; HHS, July 17–30, 1 ♀, 3 ♂♂; PCR, Aug. 2–13, 1 ♀, 1 ♂; JAC, July 15, 1 ♀. Note no. 2019: MOR-B3, July 31, ♂ taken as prey of *Philanthus pulcher*. All but 2 ♀♀ and 5 ♂♂ are of the white-banded color form called *albophaleratus* Saussure; Krombein (1967) has shown that both forms can often be reared from the same trap-nest.

Symmorphus canadensis (Saussure). MOR-B, July 19–21, 2 ♀♀, one of them note no. 2109: taken as prey of *Philanthus pulcher*.

Symmorphus c. cristatus (Saussure). ELK, July 10, 1 ♂. This is a twig-nester, like the preceding species (Krombein, 1967).

Symmorphus meridionalis Viereck. MOR, July 8–Aug. 4, 3 ♀♀; PCR, Aug. 2, 1 ♂; JAC, July 15, 1 ♀; ELK, July 18, 1 ♀, note no. 2126: taken as prey of *Philanthus zebratus nitens*.

Leptochilus erubescens (Bohart). MOR, July 7–Aug. 25, 2 ♀♀, one on Sol.

Leptochilus rufinodus (Cresson). MOR, July 24, 1 ♀.

Stenodynerus anormis (Say). MOR, July 19–Aug. 3, 1 ♀, 1 ♂.

Stenodynerus kennicottianus (Saussure). MOR, July 13, 1 ♂.

Stenodynerus lucidus (Rohwer). MOR, July 4–5, 1 ♀, 1 ♂.

Stenodynerus p. papagorum (Viereck). MOR, July 12–Aug. 11, common; PCR, Aug. 13, 1 ♀; HHS, July 17, 1 ♀. Note nos. 1992 and 2098A, MOR-B, ♀ and ♂ taken as prey of *Philanthus pulcher*. Note nos. 2003, 2015, 2039, 2108, MOR-A, July 23–Aug. 11, 1964, 1967: nesting behavior.

This species nested in considerable numbers in one small area of flat, rather hard-packed sand three to five meters from the Snake River; in 1967 there were at least 30 nests here, the entrance sometimes only 2–5 cm apart. In addition, an occasional nest was noted along sandy roads and paths farther from the river. Each nest was surmounted by an entrance tube constructed of small mud pellets, the tube making a right angle to the burrow and running along the surface of the ground, usually for 1–2 cm, but one exceptional entrance tube 4 cm long was found (Fig. 23). These tubes were often destroyed by pedestrians or by heavy rains, and in at least some cases the nests were abandoned after this. The burrows of three nests excavated were vertical, measuring about 5 cm to the most shallow cell, 6–7 cm to the deepest cell. The nests excavated contained from two to five closely clustered, oblique cells, each about 5 × 9 mm in diameter. The cells were separated by mud barriers and each had a rather hard, smooth wall, probably as a result of the soil being softened with water before being removed (Fig. 27).

Females were seen descending from a considerable height with prey, landing on or near the end of the tube, and crawling in with the prey in their mandibles. There was no evidence of a closure anywhere in the tube or burrow. The egg was laid in the empty cell before prey was brought in, and was suspended by a short filament from the top of the cell. The number of prey per cell varied from 14 to 19. All were coleopterous larvae of the families Curculionidae (tribe Anthonomini) or Chrysomelidae (*Xenochalepus* sp.). All

appeared to be leafminers, and I assume the wasp removed them from the mines, but this was not observed.

Some of the larvae found in 1964 gave rise to adult wasps in May, 1965, but no parasites were reared. In July, 1967, I noted that females were often followed by satellite flies, *Senotainia trilineata* Wulp. Also, a cuckoo wasp, *Chrysis venusta* Cresson, was seen entering the entrance tube of a nest and coming out a few seconds later.

Stenodynerus taos (Cresson). MOR, Aug. 8, ♀, on Per; ELK, Aug. 4, ♀, note no. 2032: taken as prey of *Philanthus zeb-ratus nitens*.

Pterocheilus morrisoni Cresson. MOR, July 7–Aug. 3, 3 ♀♀; ELK, July 10, 1 ♀. So far as known, species of this genus nest in the ground.

Family MASARIDAE

The two species of Masaridae treated here belong to a group known to provision its cells not with paralyzed arthropods, but with pollen and nectar.

Pseudomasaris edwardsii (Cresson). MOR-B, July 8, 2 ♀♀ on dirt road; PCR, July 17, 1 ♀; ELK, Aug. 2, 1 ♂, note no. 2133: taken as prey of *Philanthus zeb-ratus nitens*. This species is known to make mud cells attached to rocks (Hicks, 1929).

[**Pseudomasaris vespoides** (Cresson). South Gate, Yellowstone National Park, mud nest on rock found Aug. 2, 1961 (Fig. 21); male emerged from this nest more than two years later, July 1963.]

Family VESPIDAE (Social wasps)

These wasps make carton nests and provision them with macerate insects of many kinds. I made no effort to collect these wasps exhaustively or to study their behavior, and I present here a mere list of the few specimens collected.

Vespula acadica (Sladen). MOR-B, Aug. 11, 1 ♀ on Per.

Vespula austriaca (Panzer). PCR, July 17, 2 ♀♀. This species lacks a worker caste and is a social parasite of other members of this genus.

Vespula consobrina (Saussure). MOR-B, July 12, 1 ♀.

Dolichovespula arctica (Rohwer). MOR-B, July 16, 1 ♀. This is also a social parasite, attacking the following species.

Dolichovespula arenaria (Fabricius). MOR, July 16–Aug. 26, 4 ♀♀, 1 ♂; PCR, July 17, 1 ♀; JAC, July 15, 1 ♀.

Dolichovespula maculata (Linnaeus). MOR, July 16–30, 3 ♀♀; PCR, Aug. 2, 1 ♀.

Dolichovespula norvegicoides (Sladen). MOR, Aug. 14, 1 ♂; PCR, July 17, 1 ♀; JAC, July 15, 1 ♀.

Family POMPILIDAE (Spider wasps)

Spider wasps nest solitarily and prey upon spiders of approximately their own size, only one spider being used per nest-cell. Thirty species have been taken in Jackson Hole, and there is reason to regard all but one (*Dipogon sayi*) as ground-nesters, or as parasites of ground-nesting Pompilidae, although several of the species have not been studied in the field.

Cryptocheilus t. terminatum (Say). MOR-B, July 24–Aug. 27, common, ♀♂ on Per; HHS, July 17–30, 1 ♀. Note no. 2170, MOR-B3, Aug. 15–27, 1967: nesting behavior.

On August 15, a female was seen entering a vertical cicada emergence hole in a bare place among grasses and herbs 30 meters from river. She entered quickly, without noteworthy searching behavior, without prey. I dug the nest on August 23 and found seven cells, at depths of from 7 to 11.5 cm, each at the end of a short

side burrow (2–7 cm long) from the cicada hole (Fig. 33). Each cell measured about 7 × 12 mm; the cicada hole was 1 cm in diameter and terminated at a depth of 17 cm. All cells were closed with a firm plug of soil; each had a paralyzed spider, venter-up, or a wasp larva or cocoon. The larvae were more or less coiled around the spider's abdomen, feeding through the side. No relationship of depth with age of cell was noted: a cocoon was found at 10 cm, larvae at 7, 8, 9, and 11.5 cm, the one egg at 10.5 cm (remaining cell contained a moldy spider). All spiders appeared to be the same species of *Lycosa*, both sexes; two which were preserved proved to be juvenile males, possibly *L. pratensis* Emerton. On August 27 the same or another female wasp was seen about a meter away plunging into a hole which proved to be a cave-in over a mammal burrow; nest-cells, if present, were not located.

Priocnemis notha navajo Banks. MOR-B, July 27–Aug. 26, 11 ♀♀, 2 ♂♂, ♀♂ on Per, ♀ on Sol, Eri; ELK, Aug. 4, 1 ♀; PCR, Aug. 2, 1 ♀, 5 ♂♂. Other subsp. of *notha* are reported to nest in the soil and use spiders of the families Lycosidae, Clubionidae, and Salticidae.

Priocnemis notha occidentis Banks. MOR-B, July 29, 2 ♀♀, on Per; PCR, Aug. 2, 2 ♀♀.

In this subspecies, characteristic of the Pacific Northwest, the abdomen of the female is wholly rufous (wholly black in *navajo*), but males are indistinguishable from *navajo*. Jackson Hole appears to represent an area of overlap of the two subspecies. Two of the females listed above have a little black on the tip of the abdomen. The following have considerable black (apical .2–.5) and are considered intergrades: MOR-B, July 29–Aug. 26, 7 females, on Per and Sol; PCR, Aug. 2. I took both subspecies and intergrades together on several occasions. The intergrades resemble *n. notha* in color, but all

males from Jackson Hole are all black and have a subgenital plate like that of *navajo* and *occidentis*.

Dipogon sayi nigrior Townes. HHS, July 17, 1 ♀. This is a twig-nester, reported as preying upon *Xysticus* (Thomisidae). *D. s. sayi* has been studied extensively and found to prey largely upon *Xysticus* and other Thomisidae (see Evans and Yoshimoto, 1962).

Ageniella blaisdelli (Fox). MOR-B, July 28-Aug. 23, 12 ♀♀, 3 ♂♂, ♀♂, on Per, ♀ on Sol; ELK, Aug. 4, 1 ♀, on Per. Prey and nesting behavior unstudied.

Ceropales maculata fraterna Smith. MOR, July 12-Aug. 26, 2 ♀♀, 3 ♂♂, ♀♂ on Sol, Eri; ELK, Aug. 4, 1 ♀; HHS, July 17, 1 ♀, 1 ♂; PCR, Aug. 2, 1 ♂. This wasp is a cleptoparasite of *Pompilus scelestus* (Peckham and Peckham, 1898) and probably of other Pompilidae.

Evagetes bradleyi (Banks). ELK, Aug. 4, 1 ♀. This may be no more than a hairy form of *hyacinthinus*. The one female taken resembles the type of *bradleyi* closely.

Evagetes crassicornis consimilis (Banks). MOR, July 4-Aug. 26, 7 ♀♀, 5 ♂♂, ♀ on Sol; ELK, Aug. 4, 3 ♀♀. The nominate subspecies is known to be a cleptoparasite of species of *Pompilus* and *Episyron* (Richards and Hamm, 1939).

Evagetes hyacinthinus (Cresson). MOR, July 18-Aug. 23, 5 ♀♀; PCR, Aug. 2, 1 ♀; HHS, July 17, 1 ♀; ELK, Aug. 4, 1 ♀. Note no. 2020F; MOR-A, Aug. 23, 1967.

Over the previous several days a number of ♀ *Episyron quinquenotatus* were seen nesting in a small sand bank only two meters from the Snake River. On this date an *Evagetes hyacinthinus* was observed digging in this same bank, apparently searching for closed nests of *Episyron*.

Evagetes padrinus padrinus (Viereck). MOR-A, July 18-Aug. 12, 9 ♀♀, 3 ♂♂; JAC, July 15, 1 ♂.

Evagetes parvus (Cresson). MOR, July 28-Aug. 14, 2 ♀♀, 2 ♂♂, ♂ on Per; ELK, Aug. 4-10, 1 ♀, 4 ♂♂; PCR, Aug. 2, 3 ♂♂; HHS, July 17, 1 ♀. A cleptoparasite of various species of *Anoplus* and *Pompilus* (Evans and Yoshimoto, 1962).

Evagetes subangulatus (Banks). MOR-B, July 12-Aug. 14, 3 ♀♀, 3 ♂♂; ELK, Aug. 4-13, 3 ♀♀, 1 ♂, ♀ on Per; HHS, July 17-30, 5 ♀♀, 2 ♂♂; PCR, 4 ♀♀, 4 ♂♂, Aug. 2-13.

Episyron biguttatus californicus (Banks). MOR-B, July 15-Aug. 26, 4 ♀♀, 2 ♂♂, ♀ on Sol, ♂ on Per; ELK, Aug. 4, 1 ♀; PCR, Aug. 2, 1 ♂. A predator on orb-weaving spiders (Wasbauer and Powell, 1962).

Episyron oregon Evans. MOR-B, July 6-Aug. 26, 4 ♀♀, 1 ♂, ♀ on Sol; PCR, Aug. 13, 1 ♂; HHS, July 17, 1 ♀. Note no. 2000, near Ashton, Idaho, July 21, 1964.

At 1600 hours, a female was seen dragging a male *Araneus trifolium* (Hentz) backward across a sandy road through a clearing in an evergreen forest. She carried it up the stems of grass and weeds several times, flying off with it but gaining little distance because of the weight of the spider. Wasp and spider were taken for identification.

Episyron q. quinquenotatus (Say). MOR-A (also B, nesting in earth piles thrown up by ground squirrels), July 4-Aug. 26, very common, ♀♂ on Sol, Per, Eri; ELK, Aug. 4-10, 2 ♀♀, 1 ♂; PCR, July 17, 1 ♂. Note nos. 2001, 2120, July 23-Aug. 16, 1964, 1967; nesting behavior.

An exceedingly common wasp throughout the summer, restricted to areas of sand or powdery earth; males often swarm over

the sand in the morning hours. I saw many females with prey and took eleven; seven were adult *Araneus patagiatus* Clerck (6 females, 1 male), and four were juvenile *Araneus*. Females commonly place the spider in the crotch of a plant while digging the nest (Figs. 6, 7). After closure, they often pick up twigs and pebbles and place them over the nest site. The nesting behavior of this species has been reported elsewhere (see Evans and Yoshimoto, 1962, and Evans, 1963b; Kurczewski and Kurczewski, 1968, have presented 238 prey records, all Araneidae, a large number of them *Araneus patagiatus*). *Senotainia trilineata* is a known parasite.

Anoplius hispidus (Dreisbach). MOR-B, July 7–15, 6 ♂♂. I have considered *hispidus* a synonym of *cylindricus* Cresson (Evans, 1951), but since the latter may be a complex of several closely related species and since the Jackson Hole specimens are close to the type of *hispidus*, I list them under this name.

Anoplius percitus Evans. PCR, Aug. 2, 1 ♀. This is the westernmost record for this species.

Anoplius tenebrosus (Cresson). MOR, July 4–Aug. 26, common, ♀♂ on Sol, Per; also common throughout summer at ELK, JAC, PCR, HHS.

Females taken in early July often have tattered wings, suggesting that they overwinter as adults; males and freshly emerged females appear about July 20; a mating pair was taken on August 2. This species is known to prey upon Lycosidae and Thomisidae (Evans and Yoshimoto, 1962). Throughout its range the females emerge early in the season. A previously unpublished record from Gull Lake, Michigan, reveals that females take spiders very early in the season in that state (May 12, 1967; immature *Lycosa baltimoriana* Keys.). A second previously unpublished note (no. 1899, Lexington, Massachusetts, June 30, 1963) indicates that this species

suspends its prey from the crotch of a plant in the manner of *Episyron quinquenotatus* and other species (prey: *Thanatus formicinus* (Oliv.), female Thomisidae).

Anoplius ithaca (Banks). MOR-A, July 16, 1 ♀. Known to prey upon Lycosidae along watercourses (Evans and Yoshimoto, 1962).

Anoplius imbellis Banks. MOR-A, July 4–Aug. 14, 2 ♀♀, 6 ♂♂; HHS, July 11, 1 ♀. Also known to prey upon Lycosidae along watercourses (Wasbauer, 1957).

Anoplius dreisbachi Evans. MOR-B, Aug. 1–15, 1 ♀, 2 ♂♂, ♀♂ on Per; HHS, July 17–30, 2 ♂♂.

Pompilus angularis (Banks). MOR-A, July 4–Aug. 14, 9 ♀♀, 3 ♂♂; ELK; Aug. 4–13, 2 ♀♀; PCR, Aug. 2, 2 ♀♀, 1 ♂; JAC, July 25, 1 ♂. Note nos. 1801, Aug. 1961, and 1986, July 12, 1964.

This species preys upon Salticidae (five records), Gnaphosidae (one record), and Thomisidae (one record) (Evans, 1959, 1963b; Wasbauer and Powell, 1962). It is a common species on sand flats along the Snake River. Number 1986 was dragging a spider (*Pellenes* sp. female) backward over the ground, grasping the base of the spider's hind legs in the common manner of Pompilidae. She ascended grass stems on several occasions, and at these times grasped one of the more anterior legs and dragged the prey up with its anterior end forward. She flew off from grass blades with her spider but gained little distance because of the weight of the prey. On one occasion she left the spider in a crotch 3 cm high while she searched about. The nest of the species has never been found.

Pompilus anomalus (Dreisbach). JAC, July 15, 1 ♂. Known to prey upon *Xysticus* (Thomisidae) (Wasbauer and Powell, 1962).

Pompilus occidentalis (Dreisbach). MOR, July 11–Aug. 8, 9 ♀♀, 13 ♂♂, ♀♂ on Per, Eri; ELK, Aug. 4–13, 2 ♀♀; PCR,

Aug. 13, 1 ♀; HHS, July 17–30, 5 ♀♀, 4 ♂♂. This species makes a short burrow in friable soil in wooded areas, provisioning the nest with *Pardosa* (Lycosidae) (Powell, 1957; Evans, 1963b).

Pompilus dakota (Dreisbach). MOR-B, July 16–Aug. 16, 8 ♀♀, 1 on Per; ELK, Aug. 4, 1 ♀; PCR, Aug. 2–13, 3 ♀♀.

Pompilus arctus Cresson. MOR-B, July 6–29, 1 ♀, 2 ♂♂, ♀ on Per; ELK, Aug. 4, 1 ♀, on Per; PCR, July 17–Aug. 2, 2 ♀♀, 2 ♂♂; HHS, July 17–30, 2 ♀♀. This species nests in a short burrow in sandy soil, usually in woodlands; the prey consists of Lycosidae, Gnaphosidae, Amaurobiidae, and Clubionidae (Evans and Yoshimoto, 1962).

Pompilus scelestus Cresson. MOR, PCR, HHS, ELK, common July 4–Aug. 26, chiefly on sandy soil, ♀♂ on Sol, Per, Eri. Note no. 2156, ELK, Aug. 16, 1967.

A female was seen at 1045 dragging a large spider backward across a sandy road. She circled about several times and then proceeded to the base of a sagebrush plant, where she placed the spider beneath the basal leaves of a nearby *Eriogonum* and dug into a burrow close to the base of the sagebrush. This burrow had evidently been previously prepared, as she soon came out and dragged the spider into the burrow and then made a rapid closure. She then began a new burrow only 5 cm away, at a 180° angle to the first burrow. She dug here for an hour before I captured her and dug out the first burrow. This burrow was nearly vertical and terminated in a cell at a depth of 3.5 cm. The spider had its anterior end uppermost, its legs forming a plug against which sand was packed; the egg had been laid transversely on the venter of the abdomen. Within two hours the spider had recovered fully from paralysis. It was preserved and found to be a female *Lycosa frondicola* Emerton. This species is known to prey upon Lycosidae in other parts of its range, also upon

Pisauridae and Salticidae (Evans and Yoshimoto, 1962).

Pompilus fumipennis eureka (Banks). MOR-B, July 6–23, 2 ♀♀, 4 ♂♂, ♂ on Per; HHS, July 17–30, 6 ♀♀; ELK, Aug. 4–13, 1 ♀, 2 ♂♂; PCR, July 17, 1 ♂. This wasp is known to prey on Lycosidae (Evans, 1959; Wasbauer and Powell, 1962).

Pompilus apicatus Provancher. MOR-B, July 16–30, 4 ♀♀, 1 on Per; PCR, Aug. 2, 4 ♀♀; HHS, July 17–30, 4 ♀♀. Mainly a woodland species; prey and nesting behavior unstudied.

Aporinellus completus Banks. MOR-A, July 16, 1 ♀; JAC, July 15, 2 ♀♀. A predator on Salticidae (Evans and Yoshimoto, 1962).

Aporinellus taeniatus rufus Banks. MOR-A, July 14, 1 ♀, on sand. The nominate subspecies is known to prey upon Salticidae (Evans and Yoshimoto, 1962).

Family SPHECIDAE (Digger wasps)

Sphecidae made up nearly half of the wasp fauna of Jackson Hole (91 species as compared to 99 species in 11 other families together). Digger wasps are exceedingly diverse in their nesting and predatory behavior, as the following notes will testify. They are here considered by subfamily, in the following order: Sphecinae, Pemphredoninae, Astatinae, Larrinae, Crabroninae, Nyssoninae, and Philanthinae.

Subfamily SPHECINAE

Palmodes carbo Bohart & Menke. ELK, July 28–Aug. 16, 9 ♀♀, 2 ♂♂, ♀ on Per; 1 ♂, note no. 2032; taken as prey of *Philanthus zebratus nitens*; 3 ♀♀, note nos. 2125, 2143, 2156; nesting behavior.

Several females of this species nested somewhat gregariously in the middle of a sandy road ten meters from the Snake River, July 28–Aug. 16, 1967. The nests were in powdery, fine-grained sand among

short herbs and grass tufts; they were separated by 30–50 cm. Two prey taken from females or their nests proved to be large nymphs of *Cyphoderris monstrosa* Uhler, a long-horned grasshopper of the family Gryllacrididae; a third specimen, used for rearing a larva, was also evidently a nymph of this same species. These grasshoppers are nocturnal and spend the daylight hours resting under rocks and debris. They considerably exceed the wasps in size; one wasp 18 mm long was seen carrying a grasshopper 26 mm long and undoubtedly much heavier than herself. The hopper was straddled and carried forward, held by its antennae in the wasp's mandibles. One wasp climbed an herb 15 cm high with the prey, but the latter became entangled and had to be tugged free. The prey is evidently placed in or beneath a plant while the nest entrance is cleared of sand, the nest having been dug and closed before the initiation of hunting. When the closure has been removed, the wasp carries the prey to the threshold of the burrow, enters, and pulls in the prey by its antennae. The nest is then closed with rapid scraping movements of the front legs, only two to three minutes being required for closure. Only one grasshopper was used in each of the three nests excavated.

The nest is a short, oblique burrow 6–8 cm long, leading to a large, horizontal cell only 3–4 cm beneath the surface. The hopper is placed head-in, on its side, and the egg is laid at the base of the uppermost hind coxa, its anterior end fastened at or near the coxal membrane. The egg measures 4 mm in length. The larva feeds through the coxal membrane, hollowing out the inside by means of its slender anterior portion, reaching maturity in only six days and leaving the dismembered bits of the exoskeleton of the prey.

Palmodes hesperus Bohart & Menke. ELK, Aug. 4, 1 ♀; MOR-B, July 29–Aug. 3, 2 ♀♀, one on Sol, the other nesting, note no. 2134, Aug. 3, 1967.

A single female was seen closing a nest at 1415 in powdery sandy-loam a few meters from the riverbank (MOR-B2). She flew about in an excited manner, landing on various plants briefly and then returning to the nest. She picked up small stones and pieces of leaves and put them over the closed entrance. I caught the female and dug out the nest. The burrow was 7 cm long, reaching a horizontal cell 3 cm long and 5 cm beneath the surface. There was a single grasshopper in the cell, on its side, bearing the egg of the wasp in the same position as described for *P. carbo*. The prey was a large immature female of the Mormon cricket, *Anabrus simplex* Hald (Tettigoniidae). Bohart and Menke (1961) reported immatures of this same species as prey.

Podalonia communis (Cresson). MOR, July 3–Aug. 26, very common, ♀ ♂ on Sol; PCR, Aug. 13, 1 ♂; ELK, July 10–28, 1 ♀, 2 ♂ ♂, both males note no. 2126; taken as prey of *Philanthus zebratus nitens*. Nesting behavior, MOR-A2, July 24, 1967, note no. 2114.

Female seen digging in friable sand near river's edge at 1630 (Fig. 17). She dug for 20 minutes, producing a high-pitched buzzing sound. She then walked about ten meters away and seized a paralyzed cutworm (Noctuidae) which she had evidently hidden there. She carried it over the ground, straddling it and holding it with her mandibles; she deposited it about half way to the nest and returned to the nest by a circuitous route. After entering and leaving the nest, she returned to the cutworm and carried it to the entrance, then went in and pulled the prey in from the inside. As she approached the nest, she was followed by three very small milto-grammine flies (*Hilarella hilarella* Zett.), and at the same time a larger fly (*Metopia argyrocephala* Meigen) entered the empty nest and left again. After the wasp entered, all four flies perched on small herbs overlooking the nest. I left the area after

capturing the flies, and when I dug out the nest two days later I found several maggots which had destroyed the egg of the wasp. These were not reared to maturity.

Podalonia luctuosa (Smith). MOR, Aug. 10, 1 ♀; ELK, Aug. 9, 2 ♂♂, both note no. 2145; taken as prey of *Philanthus zebratus nitens*.

Podalonia mickeli Murray. MOR, July 16–Aug. 26, 2 ♀♀, one on Sol.

Podalonia occidentalis Murray. MOR, July 4–30, 1 ♀, 3 ♂♂.

Podalonia sericea Murray. MOR, July 16–Aug. 14, 4 ♀♀, 7 ♂♂, ♂ on Eri; ELK, Aug. 4–10, 3 ♀♀. Note no. 1791, MOR-B, Aug. 1, 1961; ♀ nesting along dirt road, preparing a very shallow nest which was provisioned with a single cutworm (Fig. 18). I reported on this under the incorrect name *P. robusta* (Evans, 1963b) and also described the larva under that name (Evans, 1964).

Podalonia sonorensis differentia Murray. MOR-B, July 8–30, 1 ♀, 1 ♂.

Ammophila azteca Cameron. MOR-A, July 7–Aug. 20, abundant; ELK, July 10–Aug. 2, 4 ♀♀, 8 ♂♂; HHS, July 13–Aug. 24, 1 ♀, 1 ♂. Note nos. 1993, 1996, 2007, 2012, 2013, 2018, 2028, 2029, 2030, 2031, 2046, 2050, MOR-A2, nesting behavior; note nos. 2032, 2131, 2133, ELK, 2 ♀♀, 1 ♂ taken as prey of *Philanthus zebratus nitens*.

This is one of the commonest wasps in sandy soil in Jackson Hole. It is the only North American digger wasp known to maintain several nests simultaneously. The burrows are vertical, 3–6 cm long, terminating in a horizontal cell 2.0–2.5 cm long. The prey consists of small larvae of sawflies or moths (Geometridae, Gelechiidae, rarely small Sphingidae); the prey is carried in flight. I have published a detailed study of this species elsewhere (Evans, 1965). (See also Figs. 19, 20, 31).

Ammophila cleopatra Menke. MOR, July 16, 1 ♀.

Ammophila dysmica Menke. MOR-B, Aug. 23, 1 ♀; ELK, July 28–Aug. 22, 1 ♀, 3 ♂♂. Note no. 2169, MOR-B, Aug. 23, 1967; note nos. 2124, 2133, ELK, July 28, Aug. 2, 1967; nesting behavior. Note no. 2133, ELK: 2 ♂♂ taken as prey of *Philanthus zebratus nitens*.

This species averages slightly larger than *azteca*, but preys on caterpillars of considerably larger size, carrying them over the ground rather than in flight. Number 2169 was carrying a striped noctuid caterpillar across a dirt road, pumping her abdomen up and down rapidly as if to gain momentum thereby. On reaching a patch of herbs at the roadside, she stopped and stung the caterpillar at several points on the venter (although it appeared well paralyzed) and then malaxated it just behind the head. Number 2124 was seen carrying a green noctuid caterpillar about the same length as the wasp; she also crossed a dirt road while pumping her abdomen up and down, then made a circuitous path through some herbs by the roadside and returned to the road vibrating her wings and moving rapidly over the ground, apparently unable to lift the caterpillar in flight. After covering about 15 meters she arrived at her nest in the center of the road, put the prey down, removed the closure, and drew in the caterpillar by its anterior end. In a few minutes she came out and began picking up lumps of earth and pushing them into the burrow while buzzing loudly. I dug out the nest at 1500, before she had finished filling, and found a single caterpillar in the cell with an egg on the side of the second abdominal segment. The burrow was vertical, the cell horizontal, only 3 cm deep. I believe this nest was receiving the final closure and that this one caterpillar was large enough to nourish the wasp larva.

Ammophila harti (Fernald). MOR-A, Aug. 25, 1 ♂, on Sol.

Ammophila macra Cresson. MOR-A, Aug. 14, 1 ♀; ELK, Aug. 13, 1 ♀. Note no. 2049, MOR-A2, Aug. 14, 1954. This very large species preys upon large sphingid larvae, using a single larva per nest (Fig. 20) (Evans, 1965).

Ammophila mediata Cresson. MOR-B, Aug. 23–26, 2 ♀♀, on Sol; ELK, Aug. 2, 1 ♀, note no. 2133: prey of *Phylanthus zebratus nitens*.

[***Ammophila pilosa*** (Fernald). South Gate, Yellowstone National Park, July 31, 1961, note no. 1785. Preys on small caterpillars, chiefly Lycaenidae, and stores several per cell (Evans, 1963b)].

Ammophila stangei Menke. MOR-B, July 16–30, 1 ♀, 2 ♂♂; JAC, July 25, 2 ♂♂.

Ammophila strenua Cresson. String Lake, Aug. 3, 1961, 1 ♂.

Subfamily PEMPHREDONINAE

Mimesa uncinata Cresson. MOR, July 12–Aug. 9, 3 ♀♀, 7 ♂♂, ♂ on Per; note no. 2127, MOR-B3: 1 ♂ taken as prey of *Phylanthus pulcher*.

Mimomesa mixta (Fox). MOR, July 5–29, 1 ♀, 3 ♂♂; note nos. 1984, 2101, MOR-B3: 2 ♂♂ taken as prey of *Phylanthus pulcher*. Species of this genus and the preceding are known to prey upon leafhoppers.

Diodontus argentineae Rohwer. ELK, July 28, 1 ♀; MOR-A, July 18–Aug. 17, 10 ♀♀, 4 ♂♂. Note nos. 2113, 2116: 1 ♀, 2 ♂♂, taken as prey of *Phylanthus pulcher*; notes nos. 1991, 2004, 2161B: nesting behavior.

This is one of the most abundant wasps at MOR-A2, but I studied it only briefly. A large nesting aggregation occupied flat sand well back from the river and in well shaded areas among pine trees (Map 2). Burrow entrances were only about 1 mm in diameter; each hole had a small mound of sand (about 1 × 2 cm by 0.5 cm deep)

in front of it. When digging the nest, females appear to move the front legs synchronously, but with little movement of the abdomen; the sand is thrown only a short distance, although the wasp backs out periodically and scrapes it away from the entrance. So far as I could determine, the nest entrance is left open at all times. Females emerge from their burrows head first and fly off swiftly, returning from time to time with an aphid held in their mandibles. The aphids were mainly wingless or subalate, occasionally fully winged. They were not identified, but it appeared that only one or a few species were involved.

Burrows are oblique, terminating in a succession of small cells at a depth of from 4 to 9 cm (Fig. 32). These cells are very small, each measuring about 2 × 4 mm, and are spaced 1–3 cm apart; the maximum number found per nest was five. Thirty or more aphids are packed very tightly into each cell and an egg is glued longitudinally along the venter of one of them. One of 13 cells excavated contained a dipterous maggot, but it was not reared successfully.

It should be added that *D. argentineae* has rarely been collected since its description. However, males were compared with the type specimen in the U. S. National Museum, and I feel that Rohwer's name properly applies to the species considered here. The American species of *Diodontus* have not been revised in many years, and identification of species is therefore difficult.

Diodontus ater (Mickel). MOR-B3, July 14–Aug. 26, 3 ♀♀, 3 ♂♂; note no. 2163: 1 ♂ taken as prey of *Phylanthus pacificus*; note no. 2161A, 2172: nesting behavior.

In contrast to the preceding species, *D. ater* nested in sloping gravel banks at MOR-B3. The nest holes were left open, as in *argentineae*, and as in that species there was a small mound at the entrance of each nest. I dug out two nests and found one cell in each, at depths of 8 and

10 cm, but I may well have missed additional cells, as it was difficult to follow such small burrows in soil of this texture. The cells were provisioned with aphids very similar to those found in *argentinae* nests.

Diodontus gillettei Fox. ELK, July 10, 1 ♂; PCR, Aug. 13, 1 ♀; MOR, July 4–Aug. 17, 11 ♀♀, 8 ♂♂, several in trap; note nos. 1981, 2127: 4 ♂♂ taken as prey of *Philanthus pulcher*; note no. 2163: 2 ♀♀ taken as prey of *P. pacificus*.

Pulverro columbianus (Kohl). MOR-B, July 14–Aug. 3, 5 ♀♀, 8 ♂♂; 1 ♂ found in a spider web. This is the smallest digger wasp occurring in Jackson Hole, measuring only 3–4 mm in length. It was commonly seen flying around the ground at MOR-B2, but I was unable to locate any nests.

Pemphredon rileyi Fox. MOR, July, 1 ♀ in trap. [Also South Gate, Yellowstone National Park, Aug. 2, 1 ♀.]

Pemphredon tenax Fox. MOR, July 6–Aug. 4, 9 ♀♀, 1 ♂; JAC, July 25, 1 ♂. This is an aphid predator that nests in wood.

Stigmus americanus Packard. MOR, July, 1 ♀ in trap.

Passaloecus relativus Fox. ELK, Aug. 9, 1 ♀, note no. 2144: taken as prey of *Philanthus pacificus*; HHS, July 31–Aug. 11, 2 ♀♀; MOR-B, July 6–Aug. 23, 5 ♀♀, 3 ♂♂, note nos. 1981, 1992: 1 ♀, 1 ♂ taken as prey of *Philanthus pulcher*; also 1 ♂ taken as prey of the asilid fly *Laphria vivax* Williston.

Spilomena alboclypeata Bradley. MOR, July 18, 1 ♀.

Subfamily ASTATINAE

Astata bakeri Parker. MOR-B, Aug. 9, 4 ♂♂, all note no. 2037E: taken as prey of *Philanthus crabroniformis*.

Astata nubecula Cresson. MOR, July 16–Aug. 25, 5 ♀♀, 6 ♂♂, 1 ♂ on Eri; HHS, July 17–Aug. 11, 2 ♀♀, 1 ♂; ELK, 2–10 Aug., 2 ♀♀, 2 ♂♂; PCR, Aug. 13, 2 ♂♂. Note nos. 2032, 2133, ELK: 2 ♀♀ taken as prey of *Philanthus zebratus nitens*; note no. 2037E, MOR-B: 1 ♀ taken as prey of *Philanthus crabroniformis*. Note nos. 2105, 2121, 2140, 2166, 2175, MOR-B, July 18–Aug. 25, 1967: nesting and territorial behavior.

On July 27, two males were noted occupying perches some distance apart, one on low vegetation overlooking bare soil, another on a log about three meters from the river. The latter male occupied this perch for extended periods on three successive days, flying off in response to moving objects in the vicinity and returning quickly to resume an alert posture with antennae rigidly extended. Similar territorial behavior has been reported in other species of *Astata* (Evans, 1958).

Females nested in areas of bare, hard, stony soil. Nests were widely scattered, mostly in paths or along roads. Females spent several days (probably more than a week) at a nest, preparing several cells (maximum of eight found). Each nest had a small, splayed-out mound of soil at the entrance, which was closed between trips for prey. The burrow was oblique, leading to a group of cells, none of which appeared to be in series. The cells in five nests excavated varied in depth from 3 to 17 cm, but in any one nest the cells were of nearly the same depth (7.5 to 8.5 cm in the five cells of 2166, 10 to 12 cm in the eight cells of 2175). The cells each measured about 10 × 15 mm; the older cells in each nest appeared to be deeper than the ones prepared later. The nests were provisioned with immature stinkbugs (Pentatomidae); early in the season up to four small nymphs were used per cell, later in the season two or three larger ones. The bugs are placed in the smooth-walled cells venter-down, as in *A. unicolor* and *occidentalis* (Evans,

1958). They are carried to the nest in flight, the wasp holding the bug's antennae with its mandibles and also embracing it during flight with its legs (Fig. 8). The bug is deposited beside the nest entrance while the wasp scrapes it open. All of the more than 20 bugs taken from nests or from wasps belonged to one species, probably *Chlorochroa uhleri* Stål. One cell contained two maggots which formed their puparia a few days later and gave rise to two flies, *Senotainia trilineata* Wulp, in May, 1968. A fly captured in the field as it was trailing a prey-laden *Astata* proved to be *Hilarella hilarella* Zett.

Dryudella montana (Cresson). MOR-A, July 16–Aug. 18, 5 ♀♀, 1 ♂; PCR, Aug. 2, 1 ♀. Note no. 1782: MOR-A, July 30, 1961, nesting behavior.

This is a smaller wasp than the preceding. It nests in sandier soil and preys upon nymphs of Reduviidae, Scutelleridae, and Cydnidae. I have reported upon this species elsewhere (Evans, 1963b).

Subfamily LARRINAE

Plenoculus d. davisi Fox. MOR, July 7–Aug. 3, 8 ♀♀, 6 ♂♂; ELK, July 28–Aug. 9, 5 ♀♀. Note no. 2098, MOR-B3: taken as prey of *Philanthus pulcher*. Note nos. 1990, 2020B, 2115, 2138 (MOR), 2130, 2141 (ELK): nesting behavior.

This small wasp is abundant in Jackson Hole, nesting in friable soil in a variety of situations, both in areas A and B at MOR and along a sandy road at ELK. The burrow is only about 2 mm in diameter, but is fairly conspicuous because the entrance is usually left open and the mound unleveled. The upper part of the burrow is at an angle of about 30–45° with the surface, the lower part at a much steeper angle, often nearly 90°. The five nests excavated had from one to three cells each, the cells measuring about 4 × 6 mm and being from 5 to 8 cm deep.

The prey of this wasp consists of plant

bugs (Miridae), both adults and immatures. The prey is carried to the nest in flight, often by short, hopping flights with frequent pauses, the wasp holding the bug's beak in its mandibles and embracing the body with its legs. The following mirids were taken as prey in the numbers indicated (in some cases the association of immatures with adults is uncertain):

Campylomma verbasci (Meyer)—1 adult, 7 immatures;

Orthotylus marginatus (Uhler)—1 adult; Phylini (genus & spp. ?)—12 adults, 15 immatures;

Pilophorus amoenus Uhler—3 adults, 18 immatures.

The egg is about 1.5 mm long and is laid transversely on one of the bugs, one end attached behind a front coxa and the remainder extending off to one side of the bug. Kurczewski (1968) has provided a detailed account of the nesting behavior of this species. He found maggots in two nests, but I observed no parasitism in Jackson Hole.

Plenoculus propinquus Fox. MOR-A, July 31, 1 ♀, note no. 2020A: nesting behavior.

This species is very similar to the preceding, but may use somewhat larger prey and fewer per cell (Kurczewski, 1968). The one nest found at Jackson Hole had one cell, at a depth of 5 cm, containing three unidentified Miridae.

Solierella affinis (Rohwer). MOR, July 16–Aug. 26, 10 ♀♀, 4 ♂♂; note no. 2052: nesting behavior.

A female of this wasp was taken on August 16, 1964, entering an open hole with a bug of the genus *Nabis* (Nabidae). The burrow was 4 cm long and passed just beneath the surface, reaching a depth of only 1 cm; it may have been a pre-existing hole rather than one dug by the wasp. There were three more *Nabis* at the end of

the burrow; all four were last-instar nymphs, and actually exceeded the wasp slightly in length. Kurezewski (1967) has recently reviewed the biology of ground-nesting *Solierella*.

Solierella sayi (Rohwer). MOR, July 18–Aug. 26, 5 ♀♀, 5 ♂♂; ELK, Aug. 4, 1 ♀.

Niteloater cyanurus (Rohwer). MOR, July 16, 1 ♂.

Niteloater evansi Krombein. MOR, July 12–Aug. 22, 11 ♀♀, 16 ♂♂; JAC, July 25, 1 ♀, 1 ♂. Note nos. 1772, 1792, 2011, 2119, all MOR: nesting behavior.

I studied this very common, small wasp in some detail in 1961, and have already published an account of its biology (Evans, 1963b). Brief studies in 1964 and 1967 confirmed the fact that the prey consists exclusively of minute spiders of the genus *Dictyna* (Dictynidae). This is a minute wasp which spends much time flying about close to the ground (1–2 cm high) in the nesting area; during the morning hours males are often in the majority. The females dig their nests with synchronous strokes of the front legs and from time to time back across the mound of earth, keeping it fairly well dispersed. The entrance is kept closed much of the time. Each nest may have several cells (up to six found), the cells being only 2.5–5 cm deep. Provisioning females are often followed by satellite flies, *Senotainia trilineata*.

Pisonopsis c. clypeata Fox. MOR-B, July 11–Aug. 10, 6 ♀♀, 1 ♂; note nos. 2103, 2112, 2123: nesting behavior.

I have also published on the nesting behavior of this species (Evans, 1969). It is another predator on spiders, but utilizes small Theridiidae, including the whitish species *Chrysso nordica* (Chamberlin & Ivie) and two grayish species of *Theridion*, *rabuni* Chamberlin & Ivie and *petraeum* Koch (all females). One immature *Singa*

(Araneidae) was taken from one nest. The nest is a shallow, pre-existing hole in the ground in which cells are prepared in series, separated by small lumps of earth which are picked up nearby and carried into the burrow. The cells are only 2–4 cm deep, each containing 9–17 spiders, the egg being laid obliquely on the dorsum of one of them. The burrow entrance is left open while the female provisions (Fig. 4).

Pisonopsis triangularis Ashmead. MOR, July 23, 1 ♀.

Trypoxylon aldrichi Sandhouse. MOR, July 11–Aug. 13, 3 ♀♀, 4 ♂♂; note nos. 1981, 2098; 3 ♂♂ taken from nests of *Philanthus pulcher*, MOR-B3.

Trypoxylon frigidum Smith. MOR, July 16–Aug. 3, 2 ♀♀, 1 ♂; PCR, Aug. 13, 1 ♀. Like the preceding, this is a twig-nester that preys upon spiders.

Larropsis capax (Fox). MOR, July 16–Aug. 3, 1 ♀, 2 ♂♂; ELK, Aug. 4–10, 2 ♀♀, 2 ♂♂, 1 ♂ note no. 2032: taken as prey of *Philanthus zebrastratus nitens*. [Also common at South Gate, Yellowstone National Park, July 19–Aug. 15, 26 ♀♀, 17 ♂♂.] This wasp is reported to use camel crickets (*Ceuthophilus* sp., immature) as prey. I saw females entering holes in the ground on two occasions, but found no nests.

Tachytes sayi Banks. MOR-B, Aug. 25, 1 ♀ on Sol.

Tachysphex aethiops Cresson. ELK, Aug. 4–13, 4 ♀♀, 1 ♂; HHS, July 13, 1 ♀; MOR, July 5–Aug. 1, 6 ♀♀, 8 ♂♂, ♀ on Eri. Note no. 2019, MOR-B3: 1 ♂ taken as prey of *Philanthus pulcher*; note no. 2051: nesting behavior, MOR-A2, Aug. 16, 1964.

On friable sand only two meters from the riverbank, a female was seen trying to enter a nest that had been stepped on. She was taken and the area excavated. An immature grasshopper, *Trimerotropis* sp.

(Acrididae), about 16 mm long, was located at a depth of 6 cm. A large mass of maggots was found on the prosternum, where they had evidently destroyed the egg of the wasp. This species evidently digs its own nest in flat, friable sand, as I observed several females digging, but I did not succeed in finding an active, undamaged nest.

Tachysphex nigrior Fox. MOR, July 16–30, 1 ♀, 2 ♂♂; note no. 2110: 2 ♂♂ taken from nest of *Philanthus pulcher*, as prey; note no. 2129: 1 ♀, nesting behavior, MOR-A1, July 30, 1967.

A female was observed walking rapidly over the sand with a grasshopper slung beneath her, the wasp holding the hopper by grasping its antennae with her mandibles. She entered a patch of grass, where the ground was covered with litter, and after making a few turns entered an open hole beneath a twig. There was a small mound of sand at the entrance. Five minutes later she was seen closing the nest, and I took her and dug out the nest. The shallow cell contained only the one grasshopper, which bore an egg transversely behind the front coxae. The hopper was an immature *Melanoplus* sp. (Acrididae) measuring 9.5 mm long (not counting the hind legs), approximately the same length as the wasp. The wasp had been followed all the way to the nest by a *Senotainia*, but I noted no maggots on the prey.

Tachysphex sp. near *linsleyi* Bohart. MOR-A, July 7–Aug. 15, 3 ♀♀, 4 ♂♂; note nos. 2002, 2093, 2153: nesting behavior.

A female was seen carrying a very small grasshopper over the sand at MOR-A1, on July 12, 1967, holding it in the manner described for *nigrior*. She was followed to her nest in a small pile of sand. I dug out the nest and found two cells side by side, about 1 cm apart, at a depth of 5 cm. One contained four very small grasshoppers, the other five; the egg of the wasp was

found to be laid on the prosternum of the prey in the same manner as *nigrior*. The hoppers were all early instar *Melanoplus* sp. measuring about 4 mm long, considerably smaller than this small wasp. A second female was also taken with a small, immature *Melanoplus* on July 23.

A third female was noted at MOR-A2 on August 15 as she flew in to her closed nest entrance, holding the prey in flight with all three pairs of legs plus the usual grasp with the mandibles. She deposited the hopper at the entrance, opened the nest and went in, then came out and drew in the hopper by its antennae. I was able to find only one cell in this nest, at a depth of 3.5 cm, containing three immature grasshoppers 6–8 mm long, probably *Chloealtis conspersa* (Harris) (Acrididae).

Tachysphex tarsatus (Say). ELK, Aug. 4–10, 2 ♀♀; HHS, Aug. 11–24, 2 ♀♀; JAC, July 25, 1 ♀; MOR, 13 ♀♀, 20 ♂♂, July 4–Aug. 26, ♀♂ on Sol, Per; note nos. 2092, 2167: nesting behavior, MOR-A2, July 12–Aug. 22.

Females of this species were seen on several occasions carrying immature grasshoppers over the sand, holding the antennae of the prey with their mandibles as they straddled it. Some females moved their wings rapidly as if to gain added propulsion, but they did not lift their prey off the ground. One grasshopper, *Melanoplus* sp., measured 9.5 mm, about the same length as the wasp, while a second, probably *Trimerotropis* sp. measured 8 mm (both Acrididae). Females carrying prey often proceeded several meters over the sand, then circled about and plunged directly into the open nest entrance. The burrow is very short and evidently unicellular; the two nests excavated had a cell only 1–2 cm deep and each had only the one grasshopper. These brief observations are in accord with Williams' (1914) more detailed studies of this species, which were made in Kansas.

Tachysphex terminatus (Smith). ELK, Aug. 4, 1 ♀; PCR, Aug. 13, 1 ♀; MOR-A, July 4–Aug. 16, 5 ♀♀, 4 ♂♂; note nos. 2013, 2033; nesting behavior, MOR-A2, July 27–Aug. 5.

This species preys on small acridid grasshoppers and uses several per cell. The nest entrance is closed while the female is away. One of the two nests excavated had one cell at a depth of 3.2 cm, while the second had three cells at depths of from 4 to 4.5 cm (Fig. 30). The egg is laid across the venter of the prothorax in the usual manner of members of this genus. F. E. Kurczewski has been studying this species in detail in central New York. He has found species of *Melanoplus* to be used most commonly as prey. The mean length of the prey, based on some 900 specimens, was found to be about 6.8 mm, which is considerably less than the mean length of female wasps of this species (Kurczewski, 1966). I saved 20 prey grasshoppers from two nests in Jackson Hole; all were immature *Chorthippus curtipennis* (Harris) (Acrididae) measuring 5–9 mm (mean 6.5 mm).

Subfamily CRABRONINAE

Lindenius c. columbianus (Kohl). MOR, July 16–Aug. 16, 14 ♀♀, 7 ♂♂, ♀♂ on Per; ELK, Aug. 9, 1 ♀; JAC, July 25, 1 ♂. Note no. 2098, MOR-B, 1 ♀ taken from nest of *Philanthus pulcher*, as prey; note nos. 2047, 2144, MOR-A, 3 ♀♀, 1 ♂ taken from nest of *P. pacificus*, as prey; note no. 2053, MOR-B2, nesting behavior.

Despite the abundance of this minute species, I obtained few data on nesting behavior. Several nests excavated August 16, 1964, appeared to be incomplete. In each case the burrow was vertical, about 1.5 mm in diameter, the entrance surrounded by a rim of soil about 3 cm in diameter. One nest contained a single paralyzed chalcid wasp at a depth of 6

cm. This species is known to prey upon a variety of minute flies, bugs, and parasitic Hymenoptera (unpublished observations of author from other localities).

Crabro florissantensis Rohwer. ELK, July 10, 1 ♂; MOR-B, July 11, 1 ♂, note no. 1981; taken from nest of *Philanthus pulcher*, as prey.

Crabro largior Fox. ELK, July 28, 1 ♀.

Crabro latipes Smith. MOR, July 7–Aug. 18, 4 ♀♀, 10 ♂♂, ♀♂ on Per; HHS, July 31–Aug. 24, 6 ♀♀; ELK, Aug. 2–13, 2 ♀♀, 2 ♂♂, 1 ♂ note no. 2131; taken as prey of *Philanthus zebratus nitens*. Like other members of the genus, this is a ground-nester which preys upon flies.

Crabro pleuralis Fox. ELK, Aug. 16, 1 ♀, note no. 2155; taken from nest of *Philanthus zebratus nitens*, as prey.

Crossocerus maculiclypeus (Fox). MOR-A, July 11, 1 ♀; PCR, Aug. 13, 1 ♀, 1 ♂; ELK, Aug. 16, 1 ♀, note no. 2159; taken as prey of *Philanthus pacificus*. Note no. 1983, MOR-A1, July 11, 1964; nesting behavior.

A female was seen at 1030 plunging into an open nest entrance two meters from the bank of the Snake River. Her abdomen was held very high, at an angle to the remainder of the body, and she held prey beneath her thorax, probably by the middle legs. The burrow entrance was only 1.5 mm in diameter and there was no evidence of a mound of fresh earth around it. This nest was dug out an hour later and found to contain six cells. The cells were small, each about 2 × 4 mm, and all were between 6 and 7.5 cm deep, spaced about 1 cm apart. Each cell contained numerous small flies (18 in the one cell counted), the majority small acalyptrates (List 3). Several cells contained an egg of the wasp, in each case attached to the "throat" of the fly (ventrally, between the head and

front coxae) and extending laterad at a right angle to the body of the fly. Two larvae were reared to maturity and preserved for future study.

LIST 3

Prey Records for *Crossocerus maculiclypeus* (Fox), Jackson Hole, Wyoming

CHIRONOMIDAE

Cricotopus sp. 1
Genus and species? 1

EMPIDIDAE

Bicellaria pectinata McL. 2
Platypalpus cellarius McL. 1
Platypalpus xanthopodus McL. 1

AGROMYZIDAE

Liriomyza sp. 1
Melanagromyza sp. 6

PSILIDAE

Psila rosae Fabr. 1

EPHYDRIDAE

Hydrellia sp. 3

CHLOROPIDAE

Chlorops sp. 1
Conioscinella melancholica Beek 1

MUSCIDAE: COENOSIINAE

Genus and species? 1

Crossocerus nigricornis (Provancher). MOR, July 29, 1 ♀. This species also preys upon various small flies, but nests in hollow stems (Pate, 1944).

Crossocerus wickhamii (Ashmead). MOR, July 13–Aug. 17, 6 ♀♀, 2 ♂♂, ♀♂ on various Umbelliferae; HHIS, July 31, 1 ♀. Also nests in cavities in wood, but preys upon leafhoppers (Steyskal, 1944).

Ectemnius chrysargyrus (Lepeletier & Brullé). MOR-B, July 27–Aug. 26, 5 ♀♀, 3 ♂♂, ♀♂ on Sol, ♂ on Eri; HHIS, July 23, 1 ♀. Like many of its congeners, this species nests in cavities in wood and preys upon flies.

Ectemnius continuus (Fabricius). MOR-B, July 7–Aug. 14, 5 ♀♀, 6 ♂♂; HHIS, Aug. 24, 1 ♀.

Ectemnius corrugatus (Packard). MOR, July 7, 1 ♀, 1 ♂.

Ectemnius d. dilectus (Cresson). MOR-B, Aug. 1–26, 3 ♀♀, 3 ♂♂, all on Sol.

Ectemnius dives (Lepeletier & Brullé). MOR-B, July 6–Aug. 19, 6 ♀♀, 2 ♂♂, ♀ on Sol, Per; Note no. 2019, ♂ taken as prey of *Philanthus pulcher*.

Ectemnius lapidarius (Panzer). MOR-B, July 6–Aug. 26, 4 ♀♀, 1 ♂, ♀ on Sol; ELK, July 1–Aug. 10, 2 ♂♂.

Ectemnius nigrifrons (Cresson). MOR-B, July 7–Aug. 23, 1 ♀, 3 ♂♂, ♀ on Sol.

Ectemnius spiniferus (Fox). MOR, July 7, 1 ♂.

Ectemnius trifasciatus (Say). ELK, Aug. 4, 1 ♀; JAC, July 25, 1 ♀.

Lestica interrupta bella (Cresson). MOR-B, Aug. 1–26, 8 ♀♀, 10 ♂♂, ♀♂ on Sol, Per; JAC, July 25, 1 ♂. Nests in logs; the nominate subspecies is known to prey upon small moths (Peckham & Peckham, 1905).

Belomicrus f. forbesii (Robertson). PCR, Aug. 2, 1 ♀; MOR, July 4–Aug. 26, 8 ♀♀, 12 ♂♂, ♀ on Sol. Note nos. 2019, 2110, 2116: 2 ♀♀, 6 ♂♂, all taken as prey of *Philanthus pulcher*, MOR-B3. Note no. 2111, nesting behavior, MOR-B3, July 22, 1967.

This species was found nesting within the limits of an aggregation of *Philanthus pulcher*, which not infrequently uses it as prey. The female *Belomicrus* digs an oblique burrow by flying upward and backward periodically and dropping the soil on the ground some distance from the burrow. The one nest studied had a burrow about 10 cm long; there were four cells at a depth of about 6 cm, each provisioned with

immature or adult mirid bugs, apparently all *Orectoderus obliquus*. Two of the cells contained parasitic maggots, and from these, two adult flies (*Senotainia trilineata* Wulp) were reared the following spring. A fly of this same species was captured at the nest entrance of the wasp. A fuller report on the nesting behavior of *Belomicrus forbesii* has been presented elsewhere (Evans, 1969).

***Oxybelus emarginatus* Say.** MOR-A, July 16–28, 3♂♂. This is a ground-nesting wasp that preys on midges and other small Diptera (Krombein and Kurezewski, 1963).

***Oxybelus uniglumis quadrinotatus* Say.** MOR-A, July 4–Aug. 26, abundant, ♀♂ on Sol; ELK, Aug. 4, 1 ♀; HHS, Aug. 11, 1 ♀; JAC, July 25, 1 ♀; PCR, Aug. 2, 1 ♀, 1 ♂. Note no. 2098: 6 ♂♂ taken from nests of *Philanthus pulcher*, as prey, MOR-B3. Note nos. 1818, 2090, 2095, 2100, 2103, 2104, 2150: nesting behavior, MOR-A1, A2, July 10–Aug. 11, 1961, 1967.

There are many published reports on the nesting behavior of this widely distributed species, and I shall present only a few notes here. The nests are dug in light, friable sand by very rapid strokes of the front legs while the wasp's body is nearly perpendicular to the ground. The burrow is oblique, only about 4 mm in diameter, the soil from the burrow being allowed to remain in a small mound at the entrance. In the several nests studied, burrow length varied from 6 to 10 cm, cell depth from the surface directly above from 4 to 7 cm; the cells are small, measuring about 5 × 8 mm. In this locality the number of cells per nest varied from one to four; when more than one cell is constructed per nest, the cells are closely clustered, separated by no more than 0.5–1.0 cm (Fig. 26).

The prey is carried on the sting, which is thrust into the thorax of the fly, permitting the wasp to stand on all three pairs

of legs while opening the nest entrance. In Jackson Hole, the prey consisted of various medium-sized flies, particularly blood-sucking Rhagionidae of the genus *Symphoromyia* and various Muscidae and Anthomyidae (List 4). Many other flies taken from nest-cells, but not saved for identification, appeared to represent these same or related species. From four to eight flies are used per cell. The egg is laid under the throat of one of the flies as usual in this genus.

Several females carrying prey were seen to be followed by miltogrammine flies (*Senotainia trilineata* Wulp). Three of 15 cells excavated contained maggots. The contents of all three cells were reared successfully; two produced adult *Senotainia trilineata*, the third a single adult *Phrosinella fulvicornis* (Coq.).

LIST 4

Prey records for *Oxybelus uniglumis quadrinotatus* Say, Jackson Hole, Wyoming

RHAGIONIDAE

Symphoromyia atripes Bigot 5
Symphoromyia montana Aldrich 4

LAUXANIIDAE

Sapromyza monticola Melander 1

ANTHOMYIDAE

Hylemyia depressa Stein 6
Hylemyia lasciva Zett. 1
Hylemyia platyura Meigen 2

MUSCIDAE

Myospila mediatubunda Fabr. 2
Spilogona sp. 7

TACHINIDAE

Eulasiona comstocki Townsend 1

Subfamily NYSSONINAE

***Alysson radiatus* Fox.** MOR, July 4, 1 ♂. Members of this genus and the following prey upon leafhoppers and related insects and nest in the ground, often in damp or shaded situations.

[*Didineis nodosa* Fox. South Gate, Yellowstone National Park, Aug. 2, 1 ♂.]

Ochleroptera bipunctata (Say). JAC, July 25, 2 ♂♂. Known to prey on a variety of small Homoptera (see Evans, 1966a, pp. 75–77).

Gorytes albosignatus Fox. ELK, Aug. 4, 1 ♀.

Gorytes canaliculatus asperatus Fox. MOR-A, July 15–Aug. 14, 8 ♀♀; note nos. 1802, 1995, 2044, 2097: nesting behavior.

This species nests in fine-grained sand within a few meters of the Snake River; the nest is an oblique burrow with one or more terminal cells. The prey consists of leafhoppers, principally of the genus *Idiocerus*. In Jackson Hole the two species employed were *I. apache* Ball & Parker and *I. perplexus* Gillette & Baker. Data gathered in 1961 and 1964 have already been published (Evans, 1966a, 1968). The one nest dug out in 1967 was unicellular and very shallow, a burrow 8 cm long terminating in a cell 6 cm deep. Provisioning females were seen to be followed by miltogrammine flies, *Senotainia trilineata* Wulp, and one fly, *Metopia argyrocephala* (Mg.) was reared from a nest.

Hoplisoides spilographus (Handlirsch). MOR, July 12–Aug. 5, abundant; note nos. 1988, 1994, 1998, 2006, 2017, 2094, 2102: nesting behavior.

This species nests in coarser soil than the preceding, often in heavy clay-loam with many stones. The nest is similar to that of the preceding species (Fig. 28), but the prey consists of Membracidae, in Jackson Hole always of a single species of immature Ceresini. I obtained many more prey records in 1967 beyond those reported earlier (Evans, 1966a: 46–49), and all represented this same treehopper. This species was unusually common in 1967, and I found two dense nesting aggre-

gations, each of 20 or more females, the nests sometimes separated by only a few centimeters. *Nysson rusticus* Cresson, reported as a possible parasite in 1966, was in 1967 actually seen digging into a *Hoplisoides* nest entrance. The flies *Senotainia trilineata* (Wulp) and *S. rubriventris* Macq. were also seen following provisioning females.

[**Hoplisoides spilopterus** (Handlirsch). South Gate, Yellowstone National Park, July 19, 1 ♀].

Dienoplus pictifrons Fox. MOR, July 11–Aug. 14, 7 ♀♀, 16 ♂♂, ♂ on Per; ELK, Aug. 4, 1 ♀; HHS, Aug. 11, 1 ♀. Note nos. 1981, 1984, 1992, 2116, all MOR-B, 1 ♀, 14 ♂♂: all taken as prey of *Philanthus pulcher*.

Nysson daeckei Viereck. MOR, July 12–Aug. 12, 3 ♀♀; ELK, July 10, 1 ♀. Note no. 2091Z, MOR-B, July 12, ♀ seen flying from one nest entrance of *Philanthus pulcher* to another, but not seen entering any nests. This is a known parasite of *Gorytes* and *Hoplisoides* and was probably attacking members of these genera, which nested in the area.

Nysson rusticus Cresson. MOR, July 7–Aug. 19, 7 ♀♀, 4 ♂♂; note nos. 1994X, 1998, 2094; several ♀♀ taken in close association with *Hoplisoides spilographus* nests, one seen entering a nest.

Nysson simplicicornis Fox. MOR, July 12, 1 ♀.

Stictiella emarginata (Cresson). MOR, July 14–Aug. 26, 4 ♀♀, 10 ♂♂, ♀♂ on Sol, ♂ on Eri. Although this is one of the larger and more common wasps in Jackson Hole, I was unable to find it nesting; the prey is reported to consist of adult moths (Noctuidae) (Gillaspay, Evans, and Lin, 1962).

Steniolia obliqua (Cresson). MOR, July 10–Aug. 26, abundant, ♀♂ on Sol, Erigeron; ELK, Aug. 4, 1 ♀. Note no. 2162,

Aug. 17, 1967, plus extensive notes taken in 1961 and 1964, summarized by Evans and Gillaspy (1964) and Evans (1966a).

This species forms massive "sleeping clusters," chiefly on low branches of lodgepole pine, and the females make shallow nests in fine-grained, powdery sandy loam at some distance from the clusters. The prey consists almost entirely of flies of the family Bombyliidae. Studies during 1964 and 1967 confirmed the fact (pointed out in Evans and Gillaspy, 1964) that species of the bombyliid genus *Villa* make up about 80 per cent of the prey (*V. sinuosa jannickeana* O. S., *V. l. lateralis* Say being used in considerable numbers, *V. alternata* Say and *V. concessor* Coq. in small numbers). Other flies used include the bombyliids *Geron* sp. and *Bombylius* sp., and the syrphid *Pipiza calcarata* Lowe. Natural enemies include the chrysidid wasp *Parnopes edwardsii* (Cresson) and the flies *Taxigramma heteroneura* (Mg.) and *Hilarella hilarella* (Zett.), but the flies were not shown to develop successfully in the cells of this species. Further details on the biology of this species may be found in the references cited above. (See also Figs. 5, 15, 16, 25.)

Bembix americana spinolae Lepeletier. MOR-A, July 18–Aug. 26, abundant, ♀ ♂ on Sol; ELK, July 10–Aug. 13, abundant; HHS, July 23–Aug. 24, abundant. Note nos. 1793, 1820, 1987, 2005, 2009, 2010, 2014, 2043, 2107, 2122, 2168 (MOR-A2); 2142, 2158 (ELK); 2168A (HHS): all nesting behavior, summarized in part by Evans (1966a).

This species is largely restricted to certain areas of fine-grained alluvial sand. A large nesting aggregation occurred each summer at MOR-A2 and at ELK, in both cases close to the river; at HHS an aggregation of about 50 wasps occupied a sandy road through a meadow. The nest is a simple oblique burrow with a terminal cell

(Figs. 9, 24). There was no significant difference in nest depth at the three localities; pooled data on 21 nests showed a burrow length of from 10 to 20 cm (mean 16 cm), cell depth of from 5 to 11 cm (mean 8). Parasites include the conopid fly *Physocephala texana* Will., which attacks the adults, and the miltogrammine fly *Senotainia trilineata* (Wulp); one of the latter was reared from a maggot found in a cell also containing a healthy, nearly full-grown *Bembix* larva. Other probable parasites include the chrysidid *Parnopes edwardsii* (Cresson) and the bombyliid fly *Exoprosopa dorcadion* O. S.

During 1964 deerflies were unusually abundant in area 2 at Moran, and these wasps preyed extensively upon them (*Chrysops furcatus* Walker and *C. noctifer pertinax* Will.). In 1967 these flies were relatively uncommon, and a wide variety of other flies was employed. In the three localities during the three summers of study, no less than 43 species of flies were employed as prey (List 5).

Bembix amoena Handlirsch. HHS, July 31, 1 ♀. This species is abundant in Yellowstone, nesting in coarse geyserite near hot springs and geysers (Evans, 1966a: 269–288). It preys upon a wide variety of flies. I have never taken this species within Grand Teton National Park.

LIST 5

Flies employed as prey by *Bembix americana spinolae* in Jackson Hole, Wyoming

<i>Species of fly</i>	<i>No. taken</i> 1964	<i>No. taken</i> 1967
STRATIOMYIDAE		
<i>Odontomyia hoodiana</i> Bigot	1	
TABANIDAE		
<i>Chrysops furcatus</i> Walker	25	
<i>C. noctifer pertinax</i> Will.	20	
<i>C. mitis</i> O. S.	2	
<i>Hybomitra osburni</i> Hine	1	
<i>H. phaenops</i> O. S.	2	

BOMBYLIIDAE

<i>Conophorus painteri</i> Priddy	1
<i>Systoechus fumipennis</i> Painter	1
<i>Villa agrippina</i> O. S.	1
<i>V. alternata</i> Say	1 2
<i>V. fulviana</i> Say	1
<i>V. sinuosa jaennickiana</i> O. S.	1 2

THEREVIDAE

<i>Thereva cingulata</i> Kroeb	6
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ASILIDAE

<i>Lasipogon cinereus</i> Cole	1
<i>Tolmerus callidus</i> Will.	6

DOLICHOPODIDAE

<i>Dolichopus crenatus</i> O. S.	1
<i>Dolichopus procerus</i> VanD.	1

SYRPHIDAE

<i>Chrysotoxum ventricosum</i>	
Loew	1
<i>Dasysyrphus analopsis</i> O. S.	1
<i>Eucodes volucris</i> O. S.	1
<i>Helophilus obscurus</i> Loew	1
<i>H. latifrons</i> Loew	2
<i>Melanostoma</i> sp.	2
<i>Metasyrphus palliventris</i>	
Curran	1
<i>M. astutus</i> Fluke	2
<i>Microdon lanceolatus</i> Adams	1
<i>Paragus bicolor</i> Fabr.	1
<i>Saeva pyrastris</i> L.	3
<i>Sphacrophoria</i> sp.	1 1
<i>Syrphus opinator</i> O. S.	8 1
<i>S. ribesii</i> L.	2 1
<i>Xylota bigelowi</i> Curran	2

SCIOMYZIDAE

<i>Renocera quadrilincata</i> Mel.	1
<i>Tetanocera plumosa</i> Loew	1

ANTHOMYIDAE

<i>Cordilura latifrons</i> Loew	3
<i>Hydrophoria divisa</i> Mg.	1
<i>Hylemyia</i> sp.	1

MUSCIDAE

<i>Helina cinerella</i> Wulp	2 1
<i>Helina latifrons</i> Zett.	2
<i>Helina troene</i> Walk.	1
<i>Pyrellia serena</i> Mg.	1
<i>Onadrolaria annosa</i> Zett.	1
<i>Spilogona</i> sp.	1

CALLIPHORIDAE

<i>Eucalliphora lilaca</i> Wlk.	1
<i>Lucilia</i> sp.	1
<i>Phormia regina</i> Mg.	1

TACHINIDAE

<i>Bonellimyia glauca</i> Brks.	4
<i>Dinera</i> sp.	3

<i>Microphthalma disjuncta</i>	
Wied.	1
<i>Nearchus duplaris</i> Reinh.	1
<i>Ptilodexia</i> sp.	1
<i>Trochilodes skinneri</i> Coq.	1

Subfamily PHILANTHINAE

Aphilanthops subfrigidus Dunning. MOR, Aug. 8, 1 ♂, on Sol; PCR, Aug. 2, 1 ♂; ELK, July 28–Aug. 13, 5 ♀♀, 4 ♂♂, note nos. 2126, 2133: 5 ♂♂ taken as prey of *Philanthus zebratus nitens*; note no. 2041: nesting behavior.

This species was found nesting in small numbers in the center of a hard dirt road at ELK on August 13, 1964. Each nest entrance had a small, well-scattered mound of soil at the entrance; the nest entrance appeared to be left open while females were hunting. Females returning with prey were often followed by miltogrammine flies (*Senotainia trilineata* Wulp), and other flies (*Metopia argyrocephala* Mg.) perched at nest entrances. One burrow was traced to 10 cm, where there was a storage cell containing six queen ants, all with intact wings. All appeared to be *Formica neogagates* Emery. A search was made for brood cells without success.

Philanthus pulcher Dalla Torre. MOR, July 8–Aug. 3, abundant, ♀♂ on Eri, Sol; ELK, July 28, 1 ♀; IHS, July 23, 1 ♀; JAC, July 15, 3 ♀♀; PCR, Aug. 2, 3 ♀♀. Note nos. 1981, 1982, 1984, 1992, 2019, MOR-B, July 11–31, 1964; note no. 2089, ELK, July 10, 1967; note nos. 2091, 2096, 2098, 2101, 2109, 2110, 2113, 2116–2118, 2127, 2160, MOR-B, July 11–29, 1967: all nesting behavior. I have already published briefly on this species (Evans, 1966c), and I hope to present a detailed comparative study of the species of *Philanthus* elsewhere. Only a few remarks on nests and prey are presented here.

This species forms dense nesting aggregations in areas of more or less bare,

moderately hard-packed clay-loam. It is an early season species, beginning its nesting activity in early July and extending into the first few days of August (1964) or until July 30 (1967). Nests are often separated by only a few centimeters, and each female makes a series of nests in the same general area, each nest occupying about seven to ten days of her life. During this time several cells are prepared, the maximum number found in one nest being six. The 49 cells excavated varied in depth from 6 to 10 cm (mean 8.3 cm). The number of prey per cell varied from 6 to 14, cells with smaller prey usually containing more specimens. A few cells contained nothing but wasps, many all bees, while the majority contained a mixture of wasps and bees, often several species mixed; on the whole, bees were slightly more plentiful than wasps in the cells, although about equal numbers of species of the two groups were utilized (List 6). I presented some preliminary notes on digging, leveling, and closure in 1966, and hope to cover these matters in more detail in a future paper. (See Figs. 10, 12, 36, 37.)

LIST 6

Prey records for *Philanthus pulcher* D. T.,
Jackson Hole, Wyoming

WASPS

71 records, 25 species

SCELIONIDAE

Scelio sp. 1 ♀

CHRYSIDIDAE

Chrysura pacifica Say 1 ♂
Elampus viridicyaneus Norton 1 ♂
Hedychridium fletcheri Bod. 1 ♀, 3 ♂ ♂
Holopyga ventralis Say 1 ♀
Omalus aeneus Fabr. 1 ♀

EUMENIDAE

Ancistrocerus catskill Saussure 1 ♂
Stenodynerus papagorum Viereck 1 ♀, 1 ♂
Symmorphus canadensis Saussure 1 ♀

SPIHECIDAE

Belomicrus forbesii Robt. 2 ♀ ♀, 6 ♂ ♂
Crabro florissantensis Roh. 1 ♂
Dienophus pictifrons Fox 1 ♀, 14 ♂ ♂
Diodontus argentinae Rohwer 1 ♀, 2 ♂ ♂
Diodontus gillettei Fox 4 ♂ ♂
Ectemnius dives Lep. & Br. 1 ♂
Lindenius columbianus Kohl 1 ♀
Mimesa uncinata Cresson 1 ♂
Mimumesa mixta Fox 2 ♂ ♂
Passaloecus relativus Fox 1 ♀, 1 ♂
Plenoculus davisii Fox 1 ♀
Oxybelus unigulmis quadrinotatus Say
6 ♂ ♂
Tachysphex aethiops Cresson 1 ♂
Tachysphex nigrior Fox 2 ♂ ♂
Tachysphex sp. 2 ♀ ♀, 7 ♂ ♂
Trypoxylon aldrichi Sandh. 3 ♂ ♂

BEEES

98 records, 23 species

COLLETIDAE

Colletes nigrifrons Titus 3 ♂ ♂
Hylaeus basalis Smith 5 ♀ ♀
Hylaeus conspicuus Metz 2 ♂ ♂
Hylaeus ellipticus Kirby 1 ♀, 4 ♂ ♂

ANDRENIDAE

Andrena melanochroa Ckll. 1 ♀
Panurginus atriceps Cresson 7 ♀ ♀, 3 ♂ ♂
Panurginus cressoniellus Ckll. 3 ♂ ♂
Perdita wyomingensis Ckll. 2 ♂ ♂

HALICTIDAE

Dialictus laevisissimus Smith 17 ♀ ♀
Dialictus ruidosensis Ckll. 1 ♀
Dialictus spp. 27 ♀ ♀
Dufourea maura Cresson 1 ♀
Dufourea scabricornis Bohart 1 ♂
Erylaeus niger Viereck 1 ♀
Halictus confusus Smith 2 ♀ ♀
Halictus tripartitus Ckll. 3 ♀ ♀
Sphecodes sp. 2 ♀ ♀

MEGACHILIDAE

Formicapis clypeata Sladen 2 ♀ ♀
Hoplitis producta Cresson 1 ♂
Osmia pentstemonis Ckll. 1 ♀
Osmia spp. 2 ♂ ♂
Stelis lateralis Cresson 1 ♂

ANTHOPHORIDAE

Nomada spp. 5♂♂

On many occasions, provisioning females were seen to be followed by female *Senotainia trilineata* Wulp, and on several occasions apparent successful larviposition on the prey was observed, usually as the wasp was about to enter the nest. A larger fly, *Phrosinella pilosifrons* Allen, was also commonly seen digging at closed nest entrances, and one fly of this species was reared from a cell (emerging in May, 1968, from a cell provisioned in July, 1967). On a number of occasions cuckoo wasps, usually *Hedychridium fletcheri* Bod., but on one occasion *Ceratochrysis trachypleura* Bohart, were seen flying from one nest entrance to another but not actually entering; once a *Senotainia* was seen following a *Hedychridium* for a minute or two! A female *Nysson daeckei* Viereck was also seen flying from one nest entrance to another.

***Philanthus crabroniformis* Smith.** MOR-B, July 22–Aug. 26, abundant. ♀♂ on Sol, ♂♂ on *Achillea*; HHS, Aug. 24, 1♀, 1♂; JAC, July 25, 1♀. Note nos. 2037, 2040, 2045, MOR-B, Aug. 8–14, 1964; note nos. 2128, 2135, 2136, 2139, 2147, 2148, 2152, 2154, 2164, 2165, 2171, 2173, 2174, 2176, MOR-B, July 29–Aug. 26, 1967; note nos. 2149, 2171A, HHS, Aug. 11, 1967; all nesting behavior.

This species forms rather diffuse nesting aggregations in hard, stony soil, nest entrance sometimes separated by 10–30 cm, but more often separated by a meter or more. Rarely I have found *pulcher* and *crabroniformis* occupying the same bare area; much more commonly *pulcher* is to be found in appreciably more sandy and less stony soil. There is virtually no seasonal overlap. In 1967 the first male *crabroniformis* appeared on July 22, and females were seen digging on July 24. However, digging of the nest takes several days, and no prey carriage was observed

until August 1, two days after the last *pulcher* was seen with prey. In contrast to *pulcher*, this species does not level the mound of soil at the nest entrance except in an irregular and incomplete manner; but at least half the nests have (at some time) one or two accessory burrows beside the true nest entrance, which is kept closed when the female is hunting. Also in contrast to *pulcher*, females usually maintain a single nest for the duration of their lives, making as many as 15 cells, and probably more (Fig. 38). The first cells are constructed closest to the entrance, and as the season progresses the burrow is lengthened and additional cells constructed on each side of the burrow progressively farther from the entrance. The final burrow length may be 70 cm or more; in any one burrow the cells tend to be at about the same depth (13–16 cm in the 15 cells of no. 2173; 9–15 cm in the 13 cells of no. 2165; range of variation of all cells 9–21 cm). The cells measure about 12 × 22 mm and are provisioned with from 12 to 24 small bees or wasps, the egg being laid on the top of the pile in the usual manner of wasps of this genus. Although this is a larger species than *pulcher*, it takes very small prey and only rarely uses wasps; about three-fourths of the 386 prey taken from nests or from wasps consisted of a single species of *Dialictus* (List 7).

LIST 7

Prey records for *Philanthus crabroniformis*
Smith, Jackson Hole, Wyoming

WASPS

6 records, 3 species

SPHECIDAE

Astata bakeri Parker 4♂♂

Astata nubecula Cresson 1♀

Pleuoculus davisi Fox 1♀

BEES

380 records, 16 species

COLLETIDAE

Hylaeus sp. 2♀♀

ANDRENIDAE

Andrena alboscillata Ckll. 1♀*Andrena* sp. 3♀♀*Perdita fallax* Ckll. 2♀♀

HALICTIDAE

Dialictus laevisimus Smith 47♀♀, 243

♂♂

Dialictus sp. 6♀♀, 17♂♂*Evylaus cooleyi* Cwfd. 1♂*Evylaus niger* Viereck 1♀, 5♂♂*Evylaus peraltus* Ckll. 2♂♂*Evylaus synthryidis* Ckll. 1♀, 2♂♂*Halictus confusus* Smith 1♀, 6♂♂*Halictus tripartitus* Ckll. 4♀♀*Halictus rubicundus* Christ 1♀, 6♂♂*Sphecodes patruelis* Ckll. 12♂♂*Sphecodes sulcatus* Ckll. 2♂♂*Sphecodes* spp. 15♂♂

This species was attacked by much the same parasites as *pulcher*, these parasites simply shifting their attention from one species to the other as the season progressed. Many provisioning females were followed by *Senotainia trilineata* Wulp, and two flies of this species emerged in May 1968 from cells collected in August 1967. *Phrosinella pilosifrons* Allen was also very commonly seen digging at closed nest entrances, and several of these were also reared from cells (Fig. 14). *Metopia argyrocephala* Mg. was observed following females and entering nests and accessory burrows, but I did not rear this species. Female *Ceratochrysis trachypleura* Bohart were seen on several occasions flying from one nest entrance to another. The flight patterns of prey-laden females followed by satellite flies have been described in an earlier section.

Philanthus zebratus nitens (Banks). ELK, July 28–Aug. 16, abundant; HHS, July 23–31, 3 ♀♀, 10 ♂♂; JAC, July 15, 1 ♂. About a third of the females collected have yellowish abdominal markings, and will thus key to *z. zebratus* Cresson, a

form of more southerly distribution than *nitens*; I question the value of these subspecific names. Note nos. 2032, 2036, 2131, 2132, 2133, 2145, 2146, 2155, all ELK: nesting behavior. Evans (1966c) discussed this species briefly.

This species was never taken at MOR, but was common along a sandy road at HHS; all studies were made on a very large colony of approximately 200 females nesting in or near a sandy road at ELK. This is a large, colorful species which makes conspicuous nest holes and preys on relatively large bees and wasps. The nests are similar in structure to those of *erabroniformis*, cells being constructed on either side of a burrow that is progressively lengthened (Fig. 39). As many as 17 cells may be made per nest, and some females, at least, appear to maintain a single nest for their life of about a month. Cell depth varies from 8 to 18 cm and is sometimes that variable within one nest, although in others all cells are at nearly the same depth (13–16 cm in the 11 cells of no. 2132). Cells measure about 12 × 20 mm and contain from three to nine (usually four to seven) fairly large bees or wasps. The mound of earth at the nest entrance tends to be somewhat spread out, but it is not leveled; a small percentage of nests have one or two (rarely three) accessory burrows. The nest entrance is usually closed while the female is out. Prey records are summarized in List 8.

LIST 8

Prey records for *Philanthus zebratus nitens* (Banks), Jackson Hole, Wyoming

WASPS

75 records, 25 species

ICHNEUMONIDAE

Diphyus sp. 4♂♂*Dusona* sp. 1♀*Eutanyacra* sp. 1♀, 1♂*Ichneumon* sp. 12♂♂*Spilichneumon* sp. 2♀♀, 8♂♂

EUMENIDAE

- Ancistrocerus adiabatus* Sauss. 1♀, 1♂
Euodynerus castigatus Sauss. 1♂
Stenodynerus taos Cresson 1♀
Symmorphus meridionalis Viereck 1♀

MASARIDAE

- Pseudomasaris edwardsii* Cresson 1♂

SPHECIDAE

- Ammophila azteca* Cameron 3♀♀, 2♂♂
Ammophila dysmica Menke 2♂♂
Ammophila mediata Cresson 1♀
Aphilanthops subfrigidus Dunning 5♂♂
Astata nubecula Cresson 2♀♀
Cereris aequalis idahoensis Scullen 1♀
Crabro pleuralis Fox 1♀
Crabro latipes Smith 1♂
Ectemnius sp. 2♀♀
Eucereis fulvipes Cresson 2♂♂
Larropsis capax Fox 1♂
Palmodes carbo Boh. & Men. 1♂
Podalonia communis Cresson 2♂♂
Podalonia luctuosa Smith 2♂♂
Tachysphex aethiops Cresson 1♂
Tachysphex sp. 2♀♀

BEES

74 records, 20 species

COLLETIDAE

- Colletes kincaidii* Ckll. 2♀♀, 3♂♂
Colletes nigrifrons Titus 3♀♀

ANDRENIDAE

- Andrena cyanophila* Ckll. 2♀♀
Andrena eriogoni Ckll. 16♀♀
Andrena (3 spp.) 4♀♀

HALICTIDAE

- Dufourea maura* Cresson 2♀♀
Halictus rubicundus Christ 1♀, 6♂♂
Lasioglossum trizonatum Cresson 1♀
Nomia sp. 1♂

MEGACHILIDAE

- Anthidium tenuiflorae* Ckll. 1♂
Hoplitis fulgida Cresson 2♀♀
Hoplitis producta interior Mich. 1♀
Megachile brevis Say 1♀, 3♂♂
Osmia calla Ckll. 3♀♀
Osmia indepressa Sandh. 1♀, 1♂

- Osmia tersula* Ckll. 5♀♀
Osmia trevoris Ckll. 12♀♀
Stelis monticola Cresson 2♀

ANTHOPHORIDAE

- Epeolus gabrielis* Ckll. 1♀
Nomada sp. 1♀

Returning females descend to the nesting area from a considerable height, often landing on the ground with an audible "plop," although when followed by *Senotainia* flies they often undertake a circuitous flight close to the ground before entering their nests (Figs. 11, 13). Provisioning females were often followed by as many as four *Senotainia trilineata* Wulp. Female *Phrosinella pilosifrons* Allen were also frequently seen digging into closed nest entrances. Both species of flies were reared from cell contents, emerging in May, 1968; however, the percentage of parasitism did not appear high, in the vicinity of 20 per cent of the cells excavated. Bombyliid flies (*Exoprosopa doreadion* O. S.) were seen ovipositing in nest entrances, and conopid flies (*Zodion fluvipes* Say) were seen following females, but I have no evidence that these species successfully parasitize *Philanthus*.

Philanthus bicinctus (Mickel). MOR-B, July 25, 1 ♀; HHS, July 23, 1 ♀.

Although this species did not nest in abundance in the areas of study, it is very plentiful at the South Gate of Yellowstone National Park, and has been studied there by Armitage (1965). This is a large, colorful species which makes very deep nests and preys primarily on bumblebees (males and workers of eight species of *Bombus*, but especially *B. bifarius* Cresson and *B. occidentalis* Greene). The male of this wasp is colored very differently than the female, and has been known as *Philanthus hirticulus* (Mickel). *Metopia argyrocephala* (Mg.) has been taken following provisioning females to their nests.

Philanthus pacificus Cresson. MOR-A, Aug. 3–26, 5 ♀♀, 6 ♂♂, ♂ on Sol; ELK, July 28–Aug. 9, 2 ♀♀, 9 ♂♂. Note nos. 2047, 2151, 2163, MOR-A; note nos. 2144, 2159, ELK: all nesting behavior.

This small species inhabits fine-grained, alluvial sand close to the riverbank or along sandy roads; at MOR there was no overlap in nesting sites with other species of the genus, but at ELK a few were nesting within the limits of the *zebratus nitens* colony. This is a late season nester and utilizes very small prey, mainly Halictidae (List 9). On no occasion did I find more than six females nesting in one area, and nest entrances were generally widely spaced. On one occasion two females were seen digging only 15 cm apart, but they attacked one another periodically. It appeared that some females made several successive nests close together, only a few centimeters apart. No more than three cells were found in any one nest, although it seems probable that more cells are occasionally constructed from one burrow (Fig. 35). Prey is often stored in the bottom of the oblique burrow, as in *pulcher* and several other species of this genus. Cells measured about 10 × 16 mm and tended to be about 4–5 cm apart; cell depth varied from 11–14 cm. The number of bees per cell varies from 8 to 15, and the egg is laid on the topmost bee in the usual manner of this genus. The mound of soil at the nest entrance is leveled thoroughly, as in *pulcher*; no accessory burrows were noted; a closure is maintained when the female is away from the nest. None of the six cells excavated appeared to be parasitized, but several *Senotainia trilineata* Wulp were seen following prey-laden females.

LIST 9

Prey records for *Philanthus pacificus*
Cresson, Jackson Hole, Wyoming

WASPS

10 records, 6 species

CHIRYSIDIDAE

Genus and species? 1

SPHECIDAE

Crossocerus maculiclypeus Fox 1♀

Diodontus ater Mickel 1♂

Diodontus gillettei Fox 2♀♀

Lindenius columbianus Kohl 3♀♀, 1♂

Passaloecus relativus Fox 1♀

BEES

58 records, 20 species

COLLETIDAE

Hylaeus sp. 1♀

ANDRENIDAE

Perdita fallax Ckll. 5♀♀, 1♂

HALICTIDAE

Dialictus laevissimus Smith 4♂♂

Dialictus ruidosensis Ckll. 1♂

Dialictus (10 spp.) 8♀♀, 30♂♂

Dufourea scabricornis Bohart 1♂

Evylaeus niger Viereck 1♂

Evylaeus synthryidis Ckll. 1♂

Evylaeus sp. 1♂

Halictus confusus Smith 2♂♂

Sphecodes sp. 2♀♀

Powell and Chemsak (1959) studied this species in California. They found it nesting in fine-grain sand and observed storage of the prey in short, oblique burrows, but they found no cells. In this area the prey consisted mainly of Halictidae and small Sphecidac, but they also found a braconid and an ichneumonid wasp to be used as prey.

Cerceris aequalis idahoensis Scullen.

ELK, Aug. 2, 1♀, note no. 2132: taken from a nest of *Philanthus zebratus nitens*.

Cerceris nigrescens nigrescens Smith.

MOR-B, July 8–Aug. 26, 5♀♀, 16♂♂, ♀♂ on Per, Sol; JAC, July 15, 1♂. Known to nest in the ground and prey on small weevils.

Eucerceris flavocincta Cresson. MOR-B, July 25–Aug. 26, 3 ♀♀, 1 ♂, ♀ on Per, ♂ on Sol; JAC, July 15, 5 ♀♀; PCR, Aug. 2, 1 ♀; HHS, Aug. 1, 1 ♂. Note no. 2137, MOR-B, Aug. 4, 1967: nesting behavior.

Female first seen on July 25, perched on a sagebrush and then plunging into a hole in a bare spot in coarse, hardpacked, stony soil only two meters from a high bank along the river. There was no mound of soil at the nest entrance. Several *Hoplisoides spilographus* also nested here. I did not see the female again, but dug out the nest August 4 and found seven cells at depth of from 7 to 10 cm (Fig. 34). The female was inside the burrow at a depth of 6 cm. The cells were well separated and the connecting burrows could not be traced. Three cells contained cocoons, two contained larvae, and one contained an egg laid longitudinally along the venter of a weevil; the contents of the seventh cell had deteriorated. Cells contained six or seven weevils each, of three species well mixed, but all of similar size and appearance. Of ten weevils identified, three were *Panscopus aequalis* (Horn), three were *Peritaxia rugicollis* Horn, and four were *Dyslobus* sp. The genus *Dyslobus* was reported as prey by Scullen (1939) in Oregon; Bohart and Powell (1956), working in California, reported a genus of weevils near *Dyslobus* to be used as prey.

Eucerceris fulvipes Cresson. MOR-B, July 28–Aug. 26, 4 ♀♀, 26 ♂♂, ♂ on Sol, Per; HHS, Aug. 11, 1 ♂; PCR, Aug. 2, 8 ♂♂; ELK, July 28–Aug. 10, 2 ♀♀, 5 ♂♂, 2 ♂♂ taken from nests of *Philanthus zebratus nitens*. Note nos. 203S, 204S, MOR-B2, Aug. 8–14, 1964: nesting behavior.

Several females were found nesting in hard, stony soil in the midst of a colony of *Philanthus crabroniformis*. In each instance the nest entrance was surrounded by a rim of soil and was left open at all times. Wasps were seen carrying weevils into

these holes, holding the prey well forward, probably with their mandibles. Two burrows were excavated. One formed about a 70° angle with the surface and was traced for 10 cm, where it terminated blindly; one cell was found at a depth of 5 cm, several centimeters from the burrow. The other nest contained five cells at depths of 9–10 cm; the cells were closely grouped, and each measured about 7 × 12 mm. Each cell contained 12–18 weevils; in two cases one of the top weevils bore an egg longitudinally along the venter. Of 59 weevils taken from the four cells, all but two were of one kind, a very small species with a pale dorsal spot, *Ceutorhynchus punctiger* Gyll. The other two specimens were slightly larger, one *Brachyrhinus ovatus* L., the other *Hyperodes* sp.

In digging out one nest, a female cuckoo wasp, *Hedychrum parvum* Aaron, was found deep in the burrow (near a female *Eucerceris*). One provisioning female was seen to be followed by a miltogrammine fly, *Taxigramma heteroneura* (Mg.).

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Plate I

Fig. 1. Study area MOR-A2, alluvial sand along Snake River near Jackson Hole Research Station (see Maps 1, 2). Fig. 2. Study area MOR-B3, a bare place in glacial outwash along a dirt road (see Map 1). Fig. 3. Study area ELK, alluvial sand along a dirt road 4 miles SW of the ELK P.O. (see Map 1). Fig. 4. Nest of *Pisanopsis clypeata*, closure removed but spiders in place, MOR-B3. Fig. 5. *Steniolia obliqua* feeding at the flowers of *Erigeron*, MOR-B.



Plate II

Fig. 6. *Episyrphus q. quinquenotatus*, female which has just suspended her spider, *Araneus potagius*, in the crotch of a plant, MOR-A. Fig. 7. Female of same species excavating burrow, MOR-A. Fig. 8. *Astata nubecula*, female holding her prey, an immature pentatomid, by the base of a front leg, MOR-B3. Fig. 9. *Bembix americana spinolae*, female closing nest (front legs in backstroke), MOR-A2. Fig. 10. *Senotainia trilineata* perched on a nail marking the nest entrance of *Philanthus pulcher*, MOR-B3.

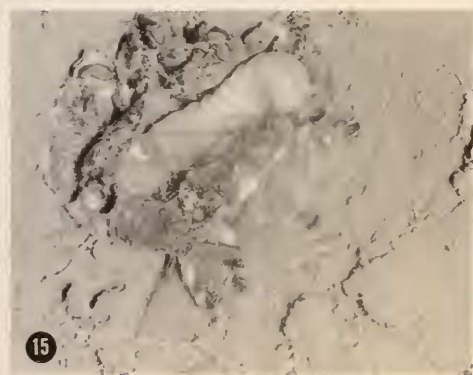
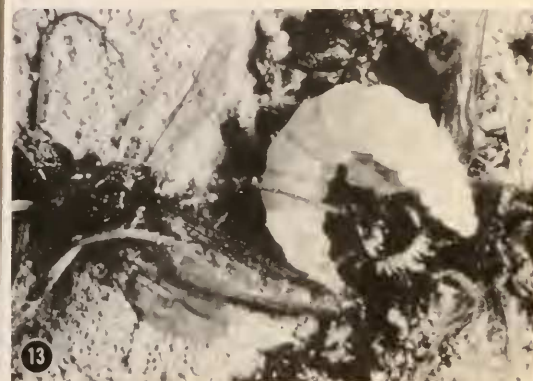


Plate III

Fig. 11. *Philanthus zebratus nitens*, female carrying prey, a male ichneumon wasp, ELK. Fig. 12. *Philanthus pulcher*, female digging at nest entrance, MOR-B3. Fig. 13. *Philanthus zebratus nitens*, larva feeding on a bee, ichneumon wasp prey on left, ELK. Fig. 14. *Phrosinella pilosifrons* digging at nest entrance of *Philanthus crabraniformis*, MOR-B3. Fig. 15. *Stenolia obliqua*, larva feeding on beefly prey in rearing tin. Fig. 16. Same species, female digging at nest entrance, MOR-A2.



Plate IV

Fig. 17. *Podalonia communis*, female digging nest, MOR-A2. Fig. 18. *Podalonia sericea*, egg on cutworm prey. Fig. 19. *Ammophila azteca*, female digging at nest entrance, MOR-A2. Fig. 20. Top, egg of *Ammophila macra* on hornworm prey; bottom, egg of *Ammophila azteca* on geometrid prey; both MOR-A2. Fig. 21. *Pseudomasaris vespoides*, four-celled mud nest found on top of rock at South Gate of Yellowstone. Fig. 22. *Euodynerus castigatus*, five-celled nest found under stone near Ithaca, N.Y. (this species also occurs in Jackson Hole). Fig. 23. *Stenodynerus papagorum*, mud turret at nest entrance, MOR-A2.

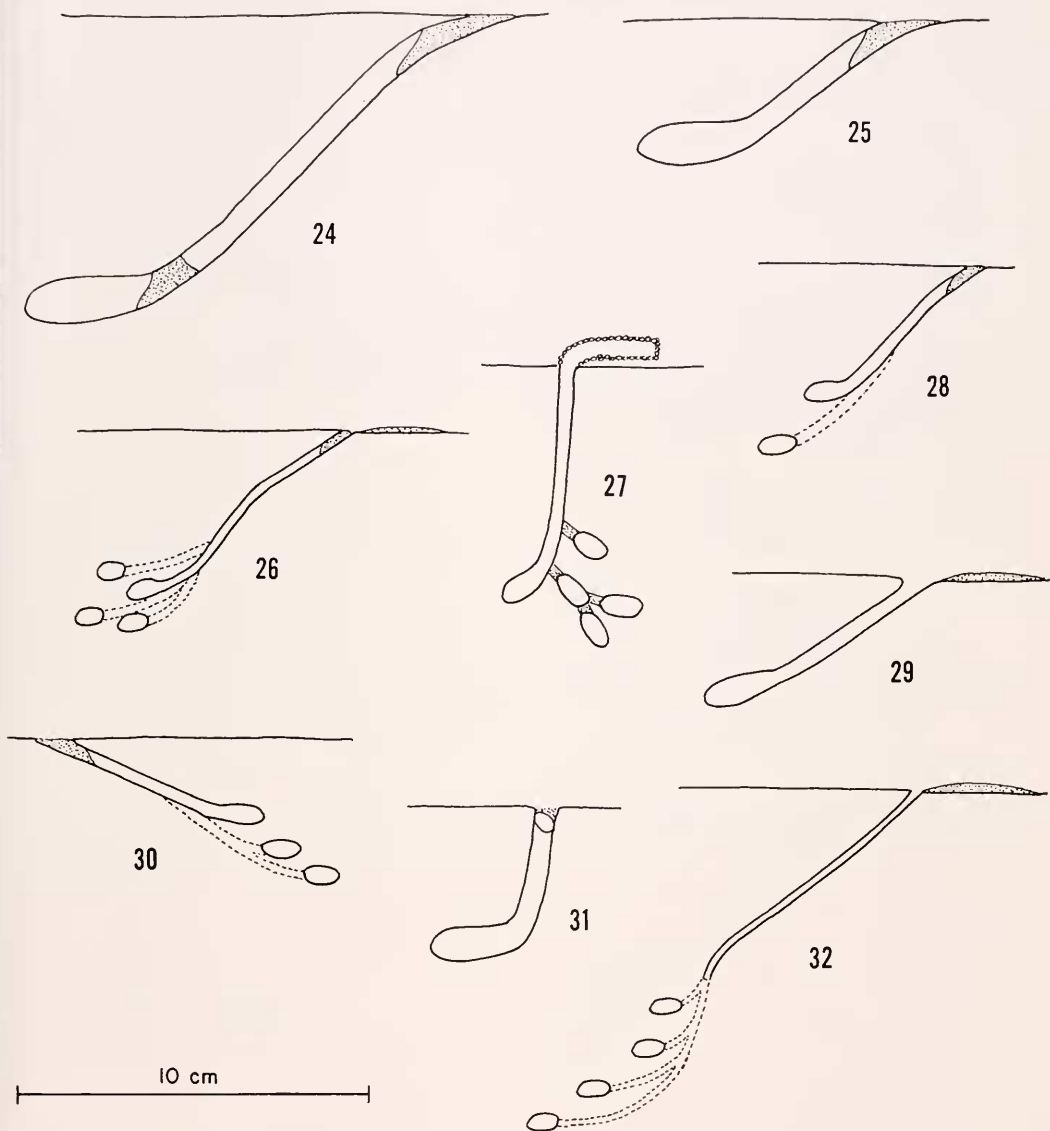


Plate V

Representative nests from study area MOR-A2, drawn to same scale (lower left). Fig. 24. *Bembix americana spinolae*, no. 2010. Fig. 25. *Steniolia obliqua*, no. 1784. Fig. 26. *Oxybelus uniglutinis quadrinotatus*, no. 2104. Fig. 27. *Stenodynerus papagorum*, no. 2015. Fig. 28. *Hoplisoides spilographus*, no. 2006. Fig. 29. *Episyron q. quinquenotatus*, no. 1771. Fig. 30. *Tachysphex terminatus*, no. 2016. Fig. 31. *Ammophila azteca*, no. 2018. Fig. 32. *Diodontus argentineae*, no. 2004. Burrows which were filled and could only be approximated are indicated by dashed lines.

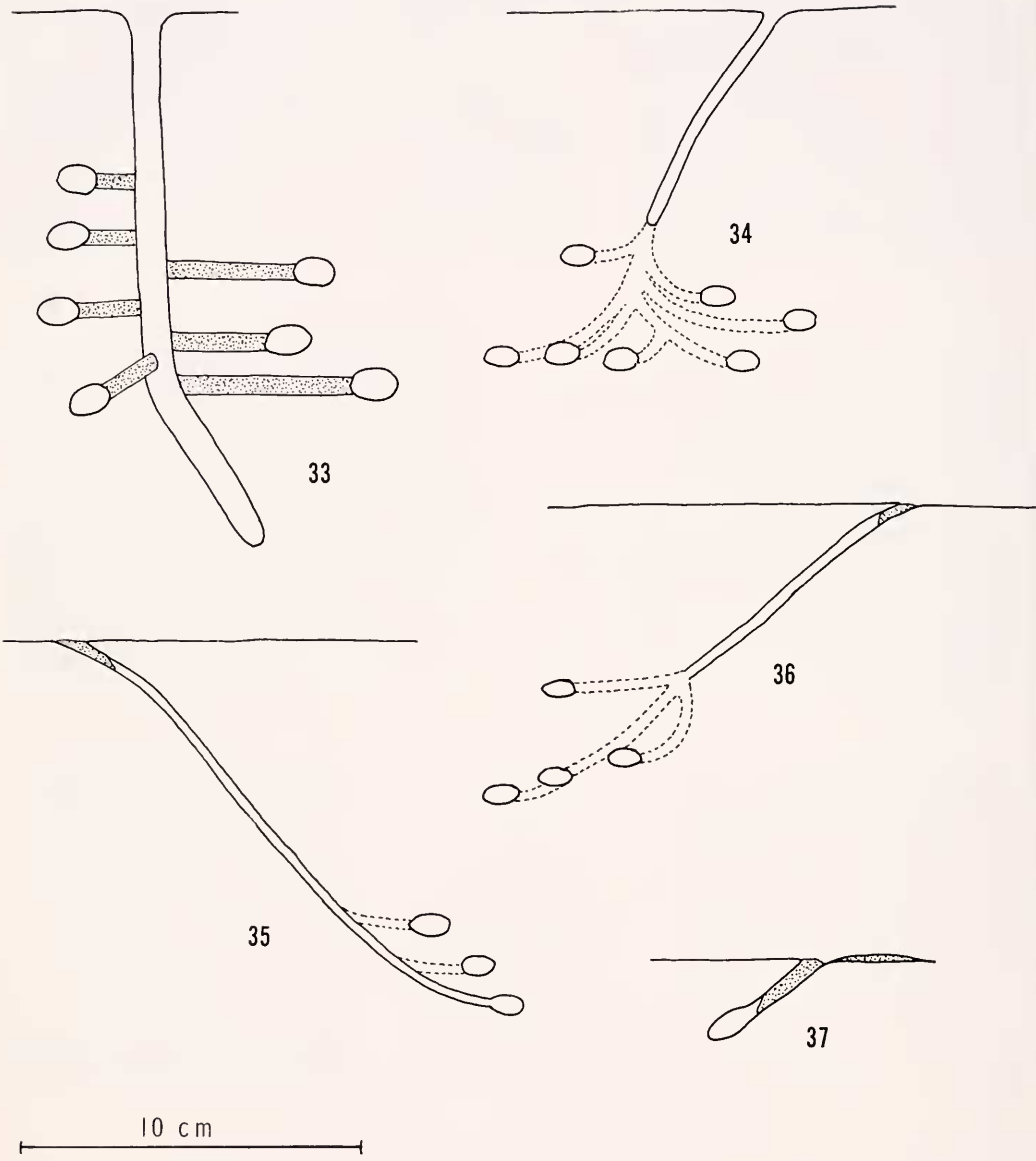


Plate VI

Representative nests of Pompilidae and Sphecidae. Fig. 33. *Cryptocheilus t. terminatum*, seven celled-nest built from walls of a cicada emergence hole, no. 2170, MOR-B3. Fig. 34. *Eucerceris flavocincta*, seven-celled nest, no. 2137, MOR-B1. Fig. 35. *Philanthus pacificus*, three-celled nest, no. 2163, MOR-A2. Fig. 36. *Philanthus pulcher*, four-celled nest, no. 2109, MOR-B3. Fig. 37. *Philanthus pulcher*, resting burrow of male, no. 2101, MOR-B3.

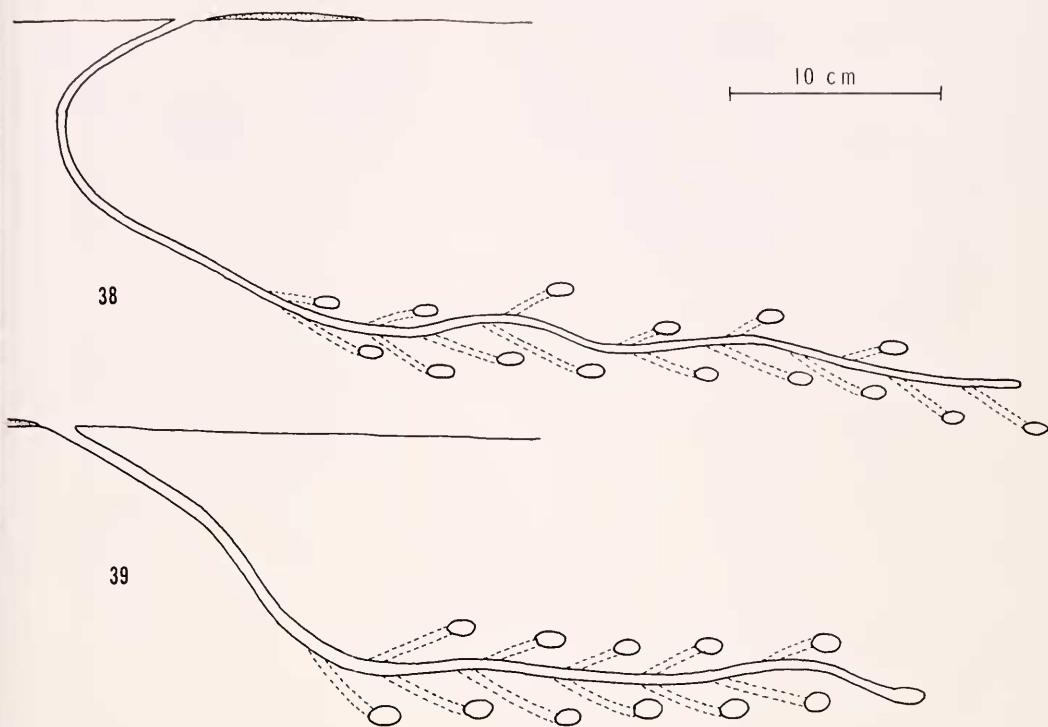


Plate VII

Fig. 38. Nest of *Philanthus crabroniformis*, no. 2173, MOR-B3. Fig. 39. Nest of *P. zebratus nitens*, no. 2155, ELK. Both somewhat diagrammatic; side-burrows to cells were packed tightly with soil and could not be traced accurately (shown as dashed lines).